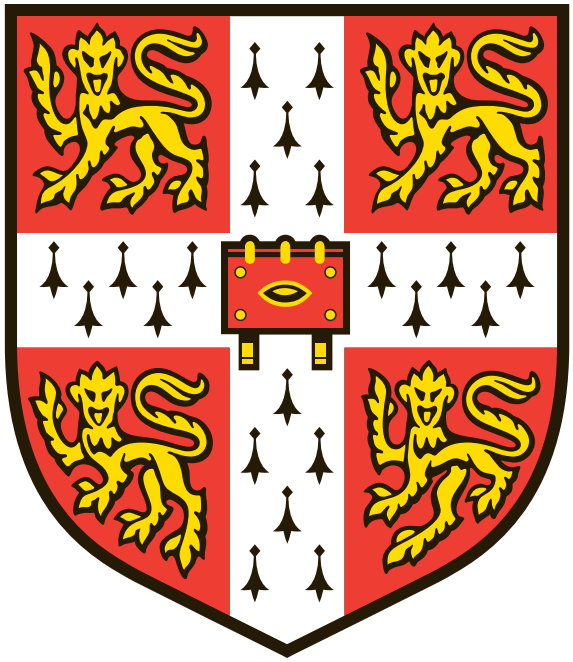
Forests of the future: ecosystem services in a forest landscape facing significant changes



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This thesis is submitted for the
degree of Doctor of Philosophy

April 2019

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my thesis has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. It does not exceed the prescribed word limit for the relevant Degree Committee.

Forests of the future: ecosystem services in a forest landscape facing significant changes

Eleanor Rosemary Tew

SUMMARY

The natural environment provides a range of benefits to people via ecosystem services. Different types of land management deliver different combinations and amounts of ecosystem services. Traditionally, many landscapes were managed to maximise the delivery of just a few benefits, such as food or timber, but this was often at the expense of other potential benefits, such as carbon sequestration or water supply. The ecosystem services approach aims to improve land management by explicitly recognising and quantifying the full range of benefits, acknowledging that all ecosystem services contribute to human wellbeing. However, despite there being much research, there is as yet limited practical application. This PhD thesis explores ecosystem service delivery in an applied forestry context, using Thetford Forest (East Anglia, UK) as a case study with the aim of generating practical recommendations for future management. As part of the UK Public Forest Estate, the delivery of a wide range of public benefits is today a central objective of forest management. However, the forest is currently facing significant changes in response to a range of issues such as climate change and disease.

I quantified the delivery of a comprehensive suite of ecosystem services for a wide range of realistic management options for the Thetford Forest landscape. Working in collaboration with the Forestry Commission (managers of Thetford Forest and my CASE partner), I tailored my research to include all the management options that are under consideration for the future of the forest. I systematically quantified how these different management options deliver nine ecosystem services: timber, carbon, deer (for game but also a management problem), water supply, soil quality, recreation, wildlife, scenic beauty and tranquillity, heritage and educational value. I conducted an in-depth analysis for each ecosystem service, using a combination of novel methodologies and adaptations of existing techniques.

It is generally acknowledged that management for ecosystem services does not always align with objectives for biodiversity conservation so I also explored how forest management affects bird diversity (as an indicator of wider biodiversity), using high-resolution remote sensing data to calculate a number of structural characteristics. Overall, wide-scale landscape heterogeneity was more important for bird diversity than within-stand heterogeneity.

In my final chapter I collated all the results for the different ecosystem services to evaluate the trade-offs and synergies between them and between different management options. I identified twelve management options that were the most efficient in terms of ecosystem service delivery. I conducted multi-criteria decision analysis to find the landscape configurations that maximise ecosystem service delivery, and investigated the effects of different values and preferences. Results were generally robust to such changes and could also align with strategies for bird conservation. The overall recommendation was for a third of the Thetford Forest landscape to be open space, half to be conifers (with a ratio of mixtures to monocultures of around 1:2) managed through a combination of both rotational clearfell and continuous-cover, and the remainder to be conifer and broadleaved mixtures, broadleaved monocultures and a small broadleaved mixture component.

This thesis illustrates a comprehensive assessment of potential ecosystem service delivery to generate recommendations for the future management of a landscape. The approach adopted here has wide application in translating ecosystem services research to practical decision making.

Preface

STATEMENT OF CONTRIBUTIONS

William Sutherland contributed to the planning of all research and commented on chapters 1 to 8. Richard Brooke read and commented on chapters 5 and 6, Jonathan Spencer read and commented on chapters 3 to 6, Edmund Tanner and Elena Vanguelova read and commented on chapters 3 and 4, Gillian Tew read and commented on chapters 1 to 8. I collected present-day soil data (chapters 3 and 4) and cultural survey responses (chapter 6). All other data were gathered from public resources or Forestry Commission datasets. Further details of contributions to individual chapters are outlined below.

Chapters 3 and 4

The Forest Research laboratory for soil analysis conducted all chemical analysis (except measuring pH for the comparison of wet and dry soil). I assisted with preparation and processing of the soil samples. Amy Eycott contributed some historical soil pH data. Edmund Tanner and Elena Vanguelova gave support in the planning of research and interpretations of result. I was assisted in the field by a number of volunteers.

Chapter 6

Benno Simmons assisted with the development of the methodology.

Chapter 7

Bird survey data were collected by the British Trust for Ornithology (BTO) and volunteers, led by Greg Conway and Ian Henderson, as part of a breeding bird survey project in Thetford Forest commissioned by the Forestry Commission. The LiDAR point cloud data were collected as part of the Breaking New Ground Heritage Lottery Project (copyright to Breaking New Ground LPS and the Forestry Commission) in 2015; further LiDAR coverage in 2017 was commissioned by the Forestry Commission. The processing of the point cloud to the canopy height model was conducted by Tom Swinfield. The plant area distribution processing of the normalised point cloud was conducted by David Milodowski. I further processed the LiDAR data and extracted the LiDAR metrics, partially based on code written by Tom Swinfield. Alison Johnston gave statistical advice.

Chapter 8

Icons designed by Freepik from Flaticon (www.flaticon.com).

PUBLICATIONS

Chapter 6 has been published in its entirety in *People and Nature*:

Tew, E.R., Simmons, B.I. & Sutherland, W.J. (2019). Quantifying cultural ecosystem services: Disentangling the effects of management from landscape features. *People and Nature* **1**: 70-86

Reflecting this, I use the pronoun 'we' rather than 'I' throughout the chapter, as published.

In addition, I have contributed to the following publications during the course of my PhD:

Jucker, T., Wintle, B., Shackelford, G., Bocquillon, P., Geffert, J. L., Kasoar, T., Jovacs, E., Mumby, H. S., Orland, C., Schleicher, J., **Tew, E. R.**, Zabala, A., Amano, T., Bell, A., Bongalov, B., Chambers, J. M., Corrigan, C., Durán, A. P., Duvic-Paoli, L-A., Emilson, C., da Silva, J. F., Garnett, E. E., Green, E. J., Guth, M. K., Hacket-Pain, A., Hinsley, A., Igea, J., Kunz, M., Luke, S. H., Lynam, W., Martin, P. A., Nunes, M. H., Ockendon, N., Pavitt, A., Payne, C. L. R., Plutshack, V., Rademacher, T., Robertson, R. J., Rose, D. C., Serban, A., Simmons, B. I., Szkokan-Emilson, E. J., Tayleur, C., Wordley, C. & Mukherjee, N. (2018). A ten-year assessment of the 100 priority questions for global biodiversity conservation. *Conservation Biology* **32**: 1457-1463

Ockendon, N., Thomas, D. H. L., Cortina, J., Adams, W. M., Aykroyd, T., Barov, B., Boitani, L., Bonn, A., Branquinho, C., Brombacher, M., Burrell, C., Carver, S., Crick, H. Q. P., Duguy, B., Everett, S., Fokkens, B., Fuller, R. J., Gibbons, D. W., Gokhelashvili, R., Griffin, C., Halley, D. J., Hotham, P., Hughes, F. M. R., Karamanlidis, A. A., McOwen, C. J., Miles, L., Mitchell, R., Rands, M. R. W., Roberts, J., Sandom, C. J., Spencer, J. W., ten Broeke, E., **Tew, E. R.**, Thomas, C. D., Timoshyna, A., Unsworth, R. K. F., Warrington, S. & Sutherland, W. J. (2018). One hundred priority questions for landscape restoration in Europe. *Biological Conservation* **221**: 198–208

Rose, D. C., Mukherjee, N., Simmons, B. I., **Tew, E. R.**, Robertson, R. J., Vadrot, A. B. M., Doubleday, R. & Sutherland, W. J. (2017). Policy windows for the environment: Tips for improving the uptake of scientific knowledge. *Environmental Science and Policy* (in press)

Acknowledgements

I would like to thank the many people who have given me invaluable help and support throughout my PhD.

Firstly, I am very grateful to my three supervisors for their support and advice: Bill Sutherland, Jonathan Spencer and Richard Brooke. Bill, thank you for your guidance in all aspects of my research, in particular for encouraging me to have big ideas and for always making time to talk things through. Jonathan, thank you for creating such a productive relationship with the Forestry Commission and impressing upon me the value of my work and its potential to make a real difference in forestry. Richard, thank you for ensuring that I have been fully integrated into the East District team and for sharing your detailed knowledge and understanding of Thetford Forest with me. Thank you also to my advisors, Andrew Balmford and Toby Gardner, for your encouragement and advice.

The collaboration with Forestry England has been the most rewarding aspect of my research. Thank you to everyone throughout the organisation who has contributed to my work and supported me in so many different ways. In particular, the East District team has been extremely supportive of my research, and many individuals have taken the time to explain their work and help me with specific tasks. I have especially enjoyed working so closely with the Planning and Environment team. You have all made me feel very welcome and valued. Thank you for fielding my never-ending questions so patiently and expertly and for sharing your knowledge so generously; I hope, in return, that my research is helpful.

It has been exciting and inspirational to work in the University of Cambridge Conservation Research Institute. In particular, thank you to past and present members of the Conservation Science Group. The advice and help I have received throughout the past few years has been invaluable but especially thank you for your friendship and making the office such a fun place to be.

I am of course grateful to my funders, NERC and Forestry England, for supporting this research. Thank you also to everyone else who is not a member of the groups above, but has nevertheless given me help, time and resources towards my research.

Finally, thank you to my close friends and family. In particular, my parents, my brother Tom, and Will, for your unconditional love and support. Your encouragement, interest and help, through the ups and downs, has been so important and I am deeply grateful.

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1 | Introduction

The natural environment provides a range of benefits to people via ecosystem services [1]. Ecosystem services are produced through natural processes, so different types of ecosystem deliver different combinations and amounts of ecosystem services. This can, of course, be influenced by human activity and land management [2]. Traditionally, many landscapes were managed to maximise the delivery of just a few benefits, such as food or timber, but this was often at the expense of other potential benefits, such as carbon sequestration or water supply [1]. This has also led to unsustainable land management and the degradation of natural capital (the abiotic and biotic components of ecosystems, including both natural resources and processes, from which ecosystem services flow) [3–5]. By recognising that all ecosystem services contribute to human wellbeing, the ecosystem services approach aims to improve land management by explicitly recognising and quantifying the full range of benefits [4].

Technically, the term ecosystem services is now used to refer to the ecosystem outputs from which people derive goods or benefits [2,6]. For example, a tree is an ecosystem service but timber is a good (which is produced through the addition of other inputs such as people and manufacturing capital). However, ecosystem services is commonly used to refer generally to goods or benefits in both the academic and non-academic literature; I follow this convention throughout this thesis, using the terms ecosystem services, goods and benefits interchangeably.

Following the Millennium Ecosystem Assessment, ecosystem services are commonly grouped into four categories: provisioning, regulating, cultural and supporting services [1]. These categories are further divided into intermediate and final ecosystem services [2,7]. Final ecosystem services lead directly to a good, and include provisioning services (which produce goods such as timber, food and water) and cultural services (which produce goods such as recreation, scenic beauty and heritage values) [8,9]. Intermediate ecosystem services underpin the delivery of final ecosystem services and include supporting services (such as nutrient cycling and primary production) [10]. Regulating services (which produce benefits such as carbon sequestration and soil quality) are often final ecosystem services, but can sometimes be intermediate ecosystem services depending on the good of interest [2,7,11,12]. This division into final and intermediate ecosystem services is important in order to avoid double-counting issues in evaluations of ecosystem service delivery [2,6].

There is a multi-layered relationship between biodiversity and ecosystem services: biodiversity can be a regulator of the ecosystem processes that generate ecosystem services (e.g. pollinators), as well as being a final ecosystem service or good in itself (e.g. a tree or bird that is valued for wildlife watching) [13]. However, not all elements of biodiversity are equally valued as goods or ecosystem services, and objectives for biodiversity conservation do not always align with management for

ecosystem service delivery [14–17]. It is therefore important that assessments of ecosystem service delivery also consider the impact on biodiversity conservation.

Over recent years, there has been considerable growth in ecosystem services research and an exponential increase in the number of academic publications that refer to it [18–20]. There is increasing recognition of the importance of the approach and it has been adopted in a number of international policy frameworks, such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the Convention on Biological Diversity [21–24]. Nevertheless, there is relatively little practical application of the ecosystem services framework, and there are several research gaps where advances could lead to increased uptake [25–28].

A key barrier to the application of the framework in practical land management or decision making is the lack of locally relevant data [29]. Many studies focus on broad-scale ecosystem service evaluations using relatively coarse land management categories [30]. While this is useful for generating policy and planning objectives at regional levels or above, studies should consider plausible management scenarios at a fine resolution scale that is relevant to management in order to most effectively inform decision making in practice [29,31–33]. The value of the ecosystem services framework lies in the consideration of multiple and varied benefits, yet most studies focus on the relatively few services that are easily quantifiable with generally a bias towards the regulating and provisioning categories [20,30]. Research must consider a comprehensive range of ecosystem services, and the relationships between them in complex environments, in order to generate an informative and complete analysis [34–36]. There is a myriad of factors that influence how different ecosystem services are valued and the benefits from different ecosystem services accrue at varying scales, from being highly localised to global [37]. An understanding of how this social context affects the results of ecosystem service assessments is an essential additional component to an understanding of how the environment affects ecosystem service delivery [34,38]. Finally, studies need to incorporate an appropriate level of complexity to realistically model a system, yet results must be simple enough to be communicated to policy makers or land managers [28,39,40]. Currently, few studies provide practical recommendations for decision making [34,41]. Stakeholder involvement throughout the research process can greatly improve its applicability, relevance and likelihood of uptake [34,38,42,43].

In this thesis, I respond to these research gaps and, using forestry as a case study, explore how the ecosystem services framework can effectively be translated into practical decision making. Forests deliver a wide range of ecosystem services and benefits, although their value to society has often been overlooked [12,44]. More than half of the world's forests – over 2 billion hectares – are classified as production or multi-use forests [45]. These forests are already managed for the production of certain ecosystem services, notably trees for timber production, but when managed sensitively they have significant potential to deliver a great range of additional benefits [46]. These include non-timber forest products, carbon sequestration, water supply, soil quality, recreation, scenic beauty and

biodiversity conservation [12]. However, to achieve this multifunctionality, forest managers need clear guidance on how management alternatives affect different ecosystem services and lead to synergies and trade-offs between them [17,47].

Forestry currently faces a plethora of challenges, including climate change, pests and disease, changes in the expectations of society and increasing recreational pressures [48–50]. In response to these issues, managed forests are undergoing significant change, as managers seek to maintain functioning ecosystems that can continue to deliver a variety of benefits [51,52]. For example, the diversification of tree species and silvicultural techniques is widely advocated as being an important strategy to increase forest resilience [53–55]. Such change also presents an opportunity to increase ecosystem service delivery and incorporate the ecosystem service framework more formally into forest planning. As forest managers explore, and test, a range of possible management options, detailed assessments and understanding of how they affect ecosystem services more broadly will generate the evidence needed to make informed decisions that lead to significant gains in ecosystem service delivery.

As the study site for my analysis I use the landscape of Thetford Forest, a large plantation (>18,500 hectares) in East Anglia, UK, currently facing significant changes. The forest was planted on low quality arable land and heathland following the First World War as part of the UK government's target to create a national strategic timber reserve [56]. The soils are low quality, with wind-blown sand overlying chalk, and are highly variable across the landscape, affecting tree species suitability [57]. The vast majority of initial planting was of Corsican pine *Pinus nigra* and Scots pine *Pinus sylvestris*, which are successful pioneer species capable of producing high volumes of timber [58]. However, at the turn of the 21st century much of the Corsican pine crop was infected with *Dothistroma septosporum*, a fungal disease that greatly decreases timber yield [49,59]. This infection, along with concerns about the increasing prevalence of tree pests and diseases generally as well as the need to adapt to a changing climate, has prompted significant re-evaluation of commercial forest management strategies in Thetford Forest [49]. In addition, the objectives of forest management have greatly changed since the initial planting of the forest almost a century ago. Thetford Forest is part of the UK Public Forest Estate, which is managed by the Forestry Commission on behalf of the general public, with the overarching objectives of 'people, nature and the economy' [60]. The ecosystem services framework maps neatly onto these aims.

The Thetford Forest landscape consists of a variety of habitats and is already widely recognised for its importance in the delivery of a range of ecosystem services, such as recreation and timber production, alongside biodiversity conservation [61]. It is predominantly a conifer plantation, although there are considerable areas of broadleaved forest and Breckland heath habitat. The open habitat network across the forest has particular biodiversity conservation importance in supporting a rare invertebrate and plant assemblage, and the forest as a whole supports internationally

important breeding populations of nightjar *Caprimulgus europaeus* and woodlark *Lullula arborea*; the forest is designated a Site of Special Scientific Interest for these features [62]. It is also part of the Breckland Special Protection Area and Special Area of Conservation [63,64]. Additionally, Thetford Forest is a regionally important recreation area [65]. It is a landscape where relatively stark trade-offs are expected between different management and habitat types in their ecosystem service delivery and biodiversity conservation potential. For example, whereas open space is important for biodiversity, it delivers no timber and negligible carbon storage compared to forested options. The Thetford Forest landscape is therefore an excellent case study for exploring how the ecosystem services framework can have practical application.

This PhD is a direct collaboration with the Forestry Commission, who is the CASE partner in the project. I worked closely with the various teams at Thetford, in particular the Planning and Environment team, to ensure that my research had applied relevance. This collaboration gave me invaluable access to both their long-term databases and records and, more importantly, to their expertise and knowledge about management of the forest. Initially, I researched the options under consideration for the future of the forest then used the detailed subcompartment database used by the Forestry Commission for management and planning to identify how the current forest landscape corresponds to a range of identified potential future management options. These options include existing and novel conifer and broadleaved tree species, in a variety of monoculture or mixture combinations, in addition to open heathland. Silvicultural options include rotational clearfell, whereby large areas of even-aged stands are felled at the same time in cycles, or continuous-cover forestry, which more closely approximates natural systems with a diversity of tree ages and selective felling. In total, I identified 37 management options, which can be aggregated into different levels of complexity depending on data availability and the methods for quantifying ecosystem service delivery. The results from my analysis therefore translate directly onto realistic management options, which greatly improves the communication and uptake of the findings.

In this thesis, I generate practical recommendations for the future management of the forest that will lead to ecosystem service and biodiversity conservation gains. In the following chapters, I quantify the potential delivery of a comprehensive range of ecosystem services for each of the identified management options. I conduct an in-depth analysis for each ecosystem service using a combination of novel methodologies and adaptations of existing techniques, and incorporate regional information to tailor the analysis to the Thetford Forest landscape (Figure 1.1). I also separately assess how management influences biodiversity conservation. Finally, I collate all this information to evaluate the relationships between these different services. The landscape configurations that will maximise ecosystem service delivery are determined using multi-criteria decision analysis (Figure 1.1). I also explore how societal preferences and values influence these conclusions, and assess how final landscape recommendations align with biodiversity conservation

objectives. By focusing on plausible scenarios at the fine-resolution scale of management, considering a comprehensive range of ecosystem services, engaging stakeholders throughout the research process, and making detailed recommendations, I address research gaps that have so far limited the practical application of the ecosystem services framework. This thesis therefore has wide application in translating ecosystem services research into land management and decision making across a range of habitats and locations.

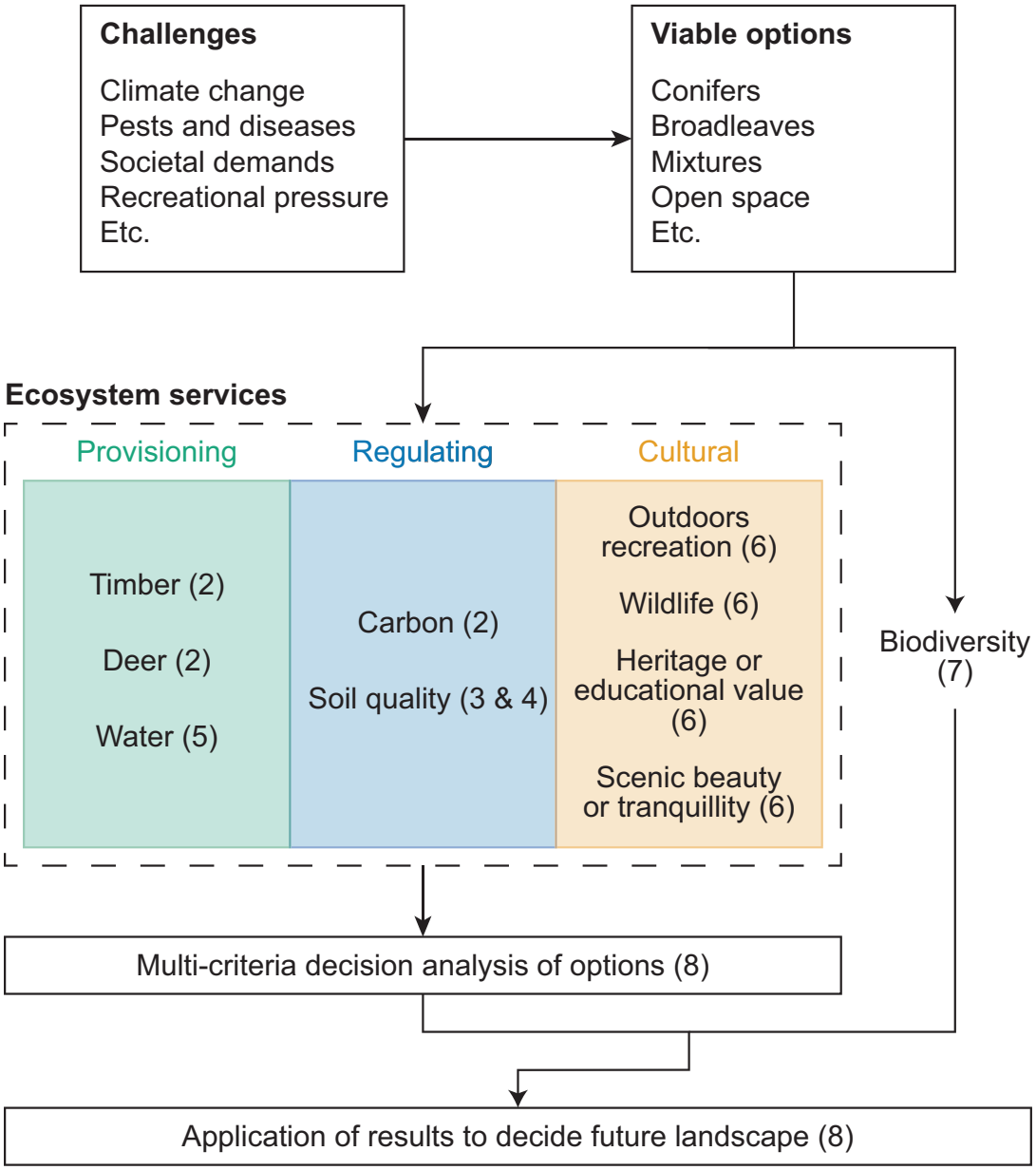

Figure 1.1: The framework followed in this thesis for the practical application of ecosystem services to decision making. A range of challenges influence which management options are viable for the future of the landscape. Ecosystem service delivery and biodiversity are quantified for each of these viable options. Given the complex relationship between ecosystem services and biodiversity, I quantify biodiversity separately to ecosystem services, although wildlife value is included as a cultural ecosystem service. A multi-criteria decision analysis compares options and is used to determine the best landscape configurations for ecosystem service delivery. In combination with the biodiversity assessment, this has direct practical application for planning the future landscape. Chapter numbers are given in brackets.

2 | The core ecosystem services in commercial forestry – timber, carbon and deer

SUMMARY

Not surprisingly, timber production has historically been the main purpose of commercial forestry, and it continues to be an essential component of multi-purpose forests today. Recently, the role of forests in carbon storage and sequestration has received global attention and new woodland planting is often pledged as a mechanism to tackle climate change. High deer densities pose a challenge to commercial forestry by causing extensive crop damage, yet they also deliver benefits such as venison income and recreational hunting. Together, timber, carbon and deer are three of the most important subjects influencing modern day forestry in the UK; in this chapter I explore how each of these ecosystem services is affected by various management options. My analysis demonstrated that conifers outperformed broadleaves in terms of timber production potential in Thetford Forest, although this difference was not so marked for carbon. Continuous-cover management strategies were better for carbon storage than clearfell strategies and this differentiation became more pronounced as the time horizon increased. Overall, deer were an ecosystem disservice, as the income generated from benefits, such as venison, was greatly outweighed by the costs associated with population management and crop damage. Broadleaved species had universally low values across all three ecosystem services. Results from the deer analysis indicate that it might be possible to select relatively high performing timber and carbon species that also experience lower deer damage, although additional data collection and trials are necessary to confirm and clarify these relationships. A mixture of clearfell and continuous-cover management strategies of a diversity of conifer species would maximise timber and carbon production, while minimising the deer ecosystem disservice.

INTRODUCTION

Forests deliver a wide range of ecosystem services [12]. However, three services stand out for being especially familiar to the concerns of modern-day foresters: timber, carbon and deer. Timber or fibre production is typically the core objective of managed forests [66]. Additionally, in recent decades forests have been recognised as being crucial in tackling climate change [67] and therefore present both an important opportunity and justification for the forestry industry. Finally, high deer densities in forests lead to a variety of practical challenges and are a fundamental issue of modern forestry [68,69]. Consequently, consideration of these three ecosystem services together represents a formal overview of key matters at the heart of commercial forestry.

In the UK, the Forestry Commission was established following the First World War to generate a strategic national timber reserve, resulting in considerable afforestation across the country [66]. Both forest cover and the active management of woodland is likely to increase further to meet increasing demands balancing timber and woodfuel, carbon mitigation targets and aspirations for resilient, multifunctional landscapes [70–73]. The multiple benefits that forests provide are increasingly recognised, but timber production remains an important component of sustainable forest management and generates essential income revenue to support it. The UK imports 80% of its wood requirements and increasing domestic timber supply (particularly of broadleaves) is a target of the recently published UK government 25 Year Environment Plan [71]. Furthermore, the UK is committed to ambitious emissions reduction targets (a net carbon account that by 2050 is 80% lower than the 1990 level); increasing carbon storage through tree planting is recognised as a simple, low-cost option to help meet them [73,74]. Clearly, forest management influences the delivery of timber and carbon benefits, so there is also great potential to increase the contributions from existing woodland through a detailed understanding of how different management strategies affect these ecosystem services [67,70,75].

Forest management is becoming more complex, with species mixtures and uneven-aged structures increasingly used as an adaptation to climate change and pressure from pests and disease [76,77]. However, the majority of global forest plantations are monospecific; in the UK, rotational clearfell management systems of conifer monocultures has thus far dominated commercial timber forestry operations [53,70]. There is consequently relatively little understanding of how such shifts to increasing forest complexity will influence timber production or carbon storage and studies that explore this are urgently needed [78]. In particular, despite increasing interest in continuous-cover forestry, very few studies have assessed the implications for carbon balances compared to more traditional management strategies [75,79]. The few existing studies suggest that continuous-cover outperforms rotational clearfell, although differences are generally small and factors such as tree growth rate can be more important than the silvicultural system [75,79–81]. Additionally, many studies focus on annual carbon sequestration rates; while important, it is often more useful to examine how management strategies affect carbon storage over time. For example, a forest stand may have an average annual sequestration rate close to zero, but still accumulate and store carbon for considerable time before being lost again through decay. The amount of carbon that can be stored over time, and the nature of storage fluctuations, is therefore an informative extra dimension to average carbon sequestration rates.

Deer densities in forests across Europe and North America are generally extremely high [82,83]. This is due to a variety of reasons including a lack of hunting pressure, few predators, the year-round availability of high quality food sources and increase in woodland cover providing safe resting areas [82,84]. Such high densities have considerable economic and ecological impacts on forestry [69]. High

grazing and browsing pressure makes crop establishment difficult and limits the range of suitable tree species, potentially compromising efforts to increase forest resilience to climate change [68]. Deer have browsing preferences for certain vegetation types, which is often dependent on the quality and quantity of other vegetation that is available, so it might be expected that they have differential effects on management options [85,86]. There is a wealth of literature demonstrating the impact of high deer numbers on woodland biodiversity. A reduction in habitat quality resulting from herbivory pressure has profound implications for plant, insect, mammal, and bird communities [69,84,87,88]. Furthermore, deer are an important vector of Lyme disease and are a significant cause of road traffic accidents [83,89,90]. Management of the deer population through culling is an essential forest activity in an attempt to diminish these impacts [83]. Nevertheless, deer also bring benefits. They are an important game species in the UK, providing recreational hunting opportunities and venison (often as a by-product of stalking or culling) [9]. They are also highly valued as a cultural ecosystem service. Therefore, deer are both an ecosystem service and disservice.

In this chapter, I quantify how a comprehensive range of forest management options in Thetford Forest affect the delivery of timber, carbon and deer ecosystem services. I develop indicators of timber production and carbon storage potential and carry out a detailed cost-benefit analysis of deer services and disservices. While I consider how management options affect each of these ecosystem services in turn, I conclude with an overall assessment of the trade-off and synergies between them and different management strategies. This is necessary for an understanding of how future forest management, which may change dramatically in response to pressures including climate change and disease, is able to meet targets for increasing timber production and emissions reductions while recognising the pervading and significant influence of deer.

METHODS

Timber

To calculate a timber production potential for each management option, I used data from general yield class curves [91]. These curves show the relationship between age of the stand and expected top height, which generally follows an asymptotic relationship. As rate of growth differs according to local conditions, potential productivity also varies, and thus curves are different for each yield class. Stands with a high yield class have faster rates of growth, and achieve greater heights, compared to stands of a low yield class. Similarly, the management of a stand (e.g. its planting spacing and thinning treatment) also affects the expected crop volume. Yield tables have been produced from these models, which predict the cumulative production volume at yearly intervals from a given stand with specified yield class, planting spacing and thinning regime. The cumulative production volume takes into account the volume produced from thinning operations, the effect of this

management on the remaining crop, and the total volume at clearfell. The yield tables can thus be used to quantify the timber provisioning service from different management options.

Yield tables have not been produced for every tree species and every planting spacing, as they have traditionally just been developed for commercial species (see Appendix table A.1 for the combinations of species and spacings with existing yield tables). Planting spacing affects the predictions for timber production, so clearly it is necessary to use the same spacing to compare different species' timber production potential. However, there is no consistent spacing that has been used universally across all species in the generation of yield tables. I selected a planting spacing of 1.5 m as my baseline for analysis, as this was the spacing for which the most species had a yield table. For species without a yield table at a planting spacing of 1.5 m, I interpolated between yield model curves using the methods outlined below. These other species fell into two categories: species with yield tables for two or more planting spacings other than 1.5 m, or species with yield tables for only one planting spacing (not 1.5 m).

Interpolation method 1: yield tables for two or more other planting spacings

For each yield class and planting spacing combination, I plotted cumulative timber volume against planting spacing. I then fitted a linear model for each yearly interval across the different planting spacings (e.g. Figure 2.1). The type of linear model fitted to the data varied according to the number of planting spacings available (two spacings = simple linear model; three spacings = squared linear model; four or more spacings = cubic linear model). I only fitted linear models for the minimum

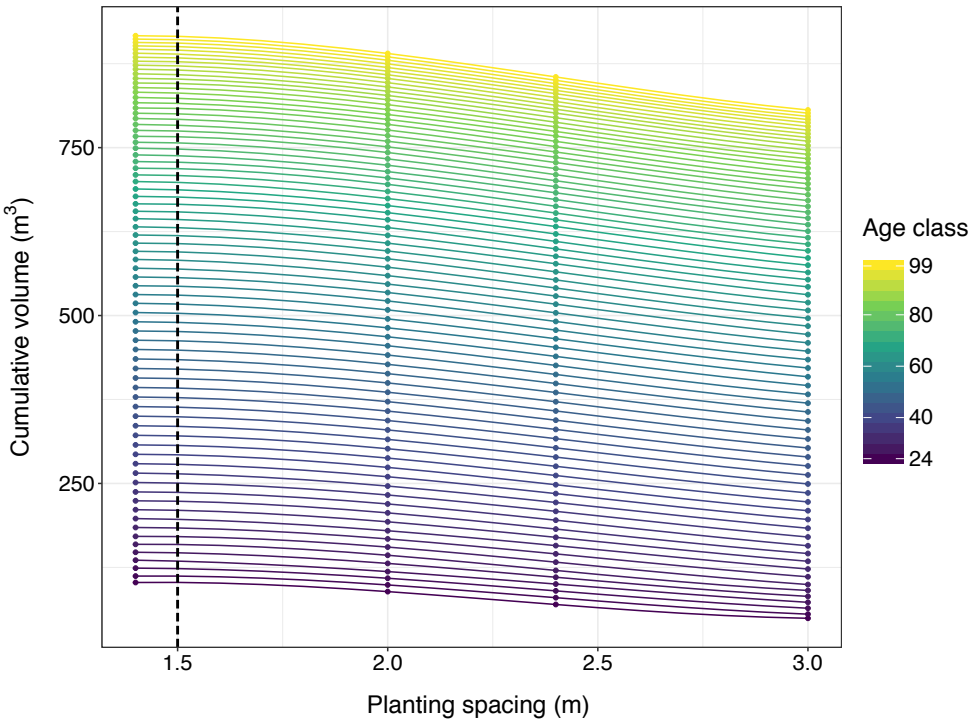

Figure 2.1: Cumulative timber volume plotted against the planting spacing for Scots pine (yield class 10). Each point indicates a datapoint extracted from existing yield tables. The curved lines are the linear models fitted to the data. The vertical dashed line indicates a planting spacing of 1.5 m, at which point values were extracted from each linear model.

age range, i.e. only the yearly intervals where there were data for each planting spacing. From each of these linear models, I extracted the cumulative volume at a planting spacing of 1.5 m for each year.

Interpolation method 2: yield tables for only one spacing (not 1.5 m)

I plotted the cumulative volume against age for every yield class and species combination where there was more than one planting spacing available (excluding poplar *Populus spp.*, where the planting spacings available were abnormally high). For each species, I fitted a family of cubic linear models that varied only by y-axis intercept for the different planting spacings (using the nls function in R) (Figure 2.2a). I found that cubic linear models gave a better fit to the data than logistic growth models. I then plotted the y-axis intercept value from each of these linear models against the planting spacing (Figure 2.2b), repeating this for each species and yield class combination (Figure 2.2c). Finally, I fitted a family of cubic linear functions for all of the y-axis intercept values, which again varied only by y-axis intercept for the different species and yield class combinations (Figure 2.2d).

For each species and yield class that had only one spacing, I fitted a separate cubic linear model (Figure 2.2e). I substituted the y-axis intercept value of this model into the family of functions for y-axis intercept values (Figure 2.2f), which enabled me to find the predicted value for a y-axis intercept at a spacing of 1.5 m (Figure 2.2g). I then substituted this y-axis intercept value into the original cubic linear model to extrapolate a curve at a planting spacing of 1.5 m (Figure 2.2h) and calculated the yearly cumulative volume.

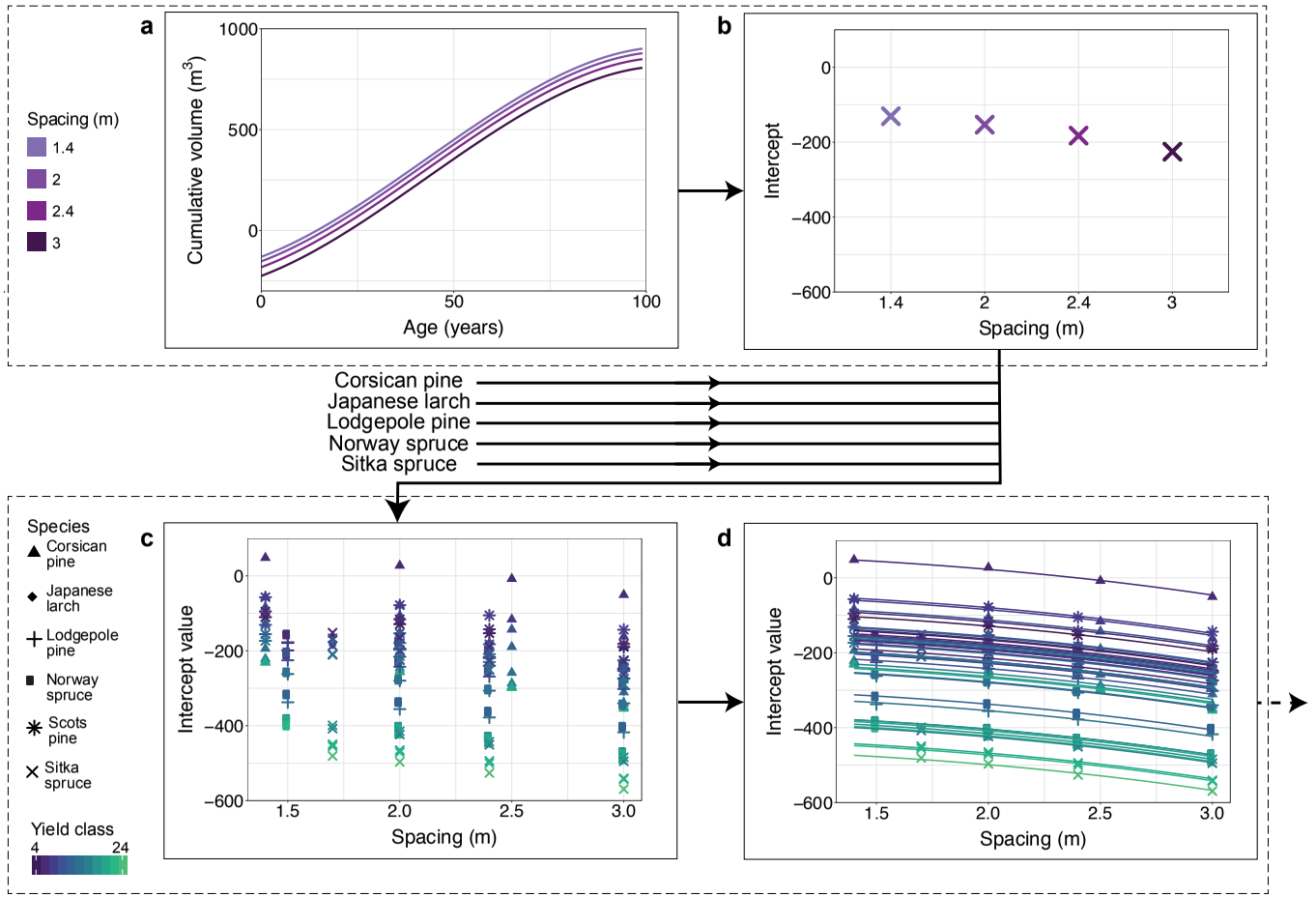

Figure 2.2: Flow diagram to show the generation of a linear model for 1.5 m planting spacing, when only one (different) planting spacing is available for the species and yield class. (a) Family of linear models for all available planting spacings for one species/yield class combination (Scots pine, yield class 10). Colours indicate different planting spacings. (b) Y-axis intercept values from part (a) plotted against planting spacing. Colours indicate different planting spacings. (c) Y-axis intercept values for all species/yield class combinations that have more than one available spacing. Symbols indicate species, colours indicate yield class. (d) All y-axis intercept values, fitted with a family of linear models (varying only by y-axis intercept for each species/yield class combination). Symbols indicate species, colours indicate yield class.

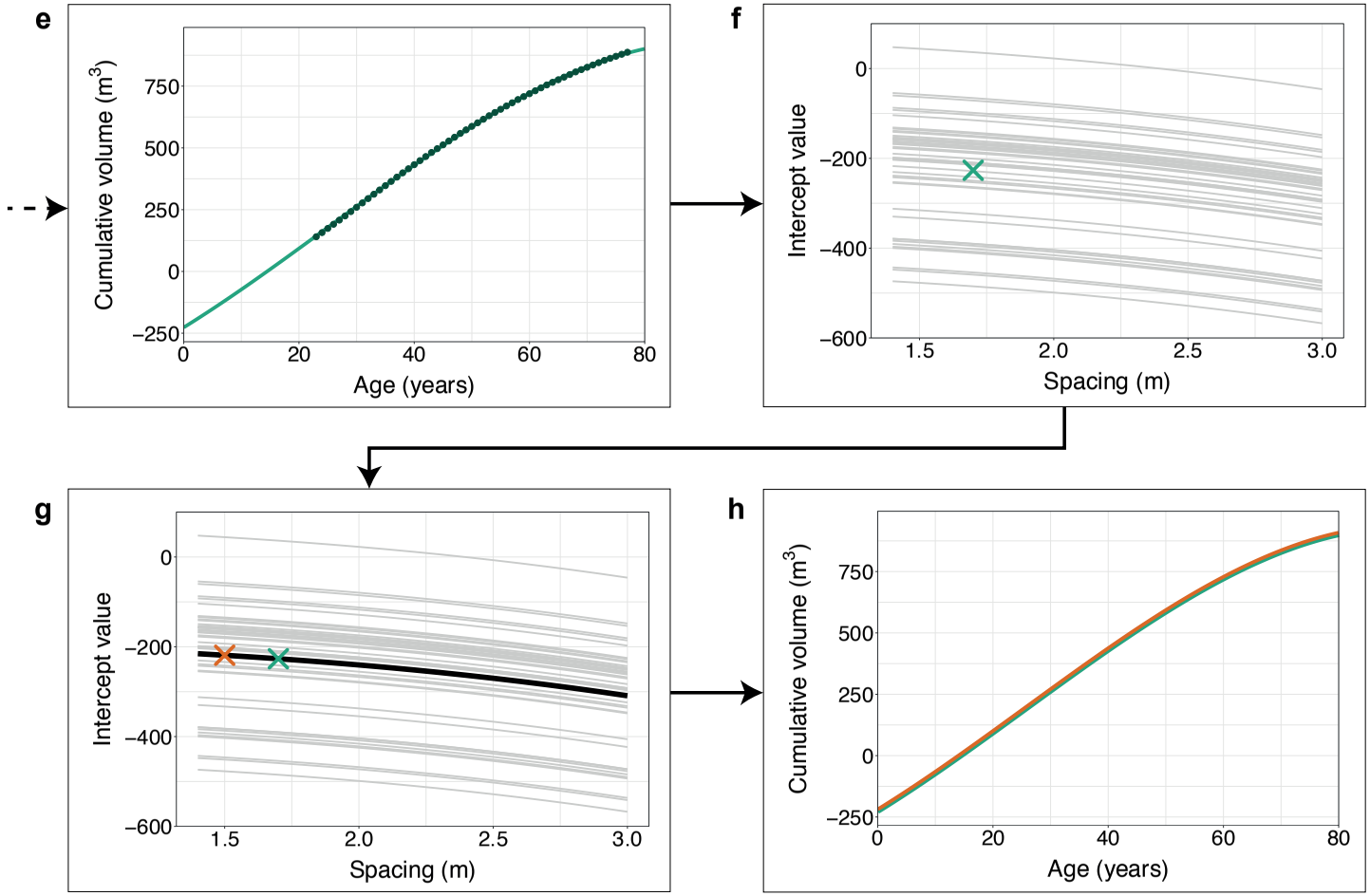

Figure 2.2 continued. (e) Linear model fitted to the target species/yield class combination with only one available planting spacing (Douglas fir, yield class 10). (f) Y-axis intercept from the target species/yield class combination plotted over the family of planting spacing and y-axis intercept linear models from (d). (g) Linear model fitted to the y-axis intercept value from the target species/yield class combination (green cross), which gives the predicted y-axis intercept value for a spacing of 1.5 m (orange cross). (h) Linear models of the target species/yield class combination for the original spacing (green) and predicted for the 1.5 m spacing according to the new y-axis intercept value from (g) (orange).

Calculation of timber production potential

The optimal and realised rotation length differs for each species and yield class. Therefore, to make comparisons between options, I divided the cumulative volume by age for each year and identified the maximum value. I took this value to be an indicator of timber production potential. For example, Figure 2.3 shows the cumulative growth curve for Scots pine (yield class 10, spacing 1.4 m) in purple and the cumulative volume divided by age in green. The timber production potential value is 9.99, which is at age 70.

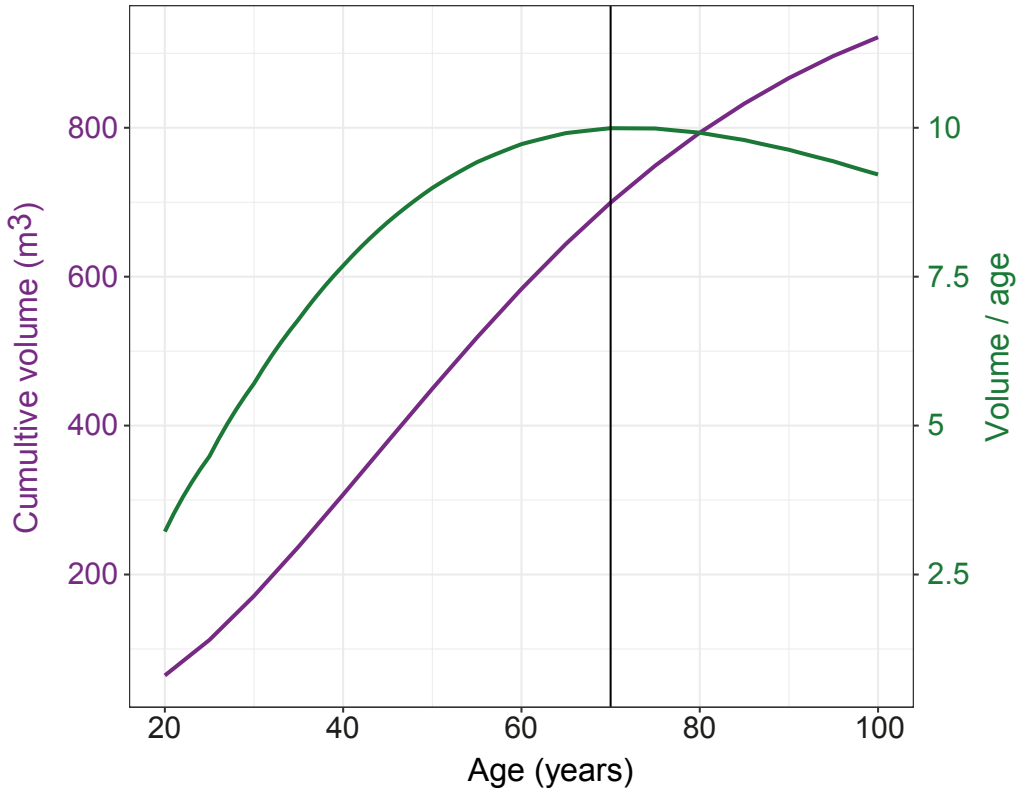

Figure 2.3: Calculation of the timber production potential for Scots pine (yield class 10, spacing 1.4 m). The purple line indicates the cumulative volume, the green line indicates the cumulative volume divided by age. The maximum volume/age is at age 70 (indicated by the vertical black line).

Method accuracy

Clearly, interpolating between existing yield curves in the manner outlined above is not ideal. Fitting linear models that vary only by y-axis intercept is not realistic, as all yield curves would begin at the graph origin. It does not realistically capture the cumulative volume throughout all ages, particularly at the lower age classes. Nevertheless, by altering the intercepts this technique does capture the variation in curves between different planting spacings around the central point of the graph, which is where the timber production potential value (maximum cumulative volume divided by age) is found. To formally test the accuracy of this technique, I removed certain planting spacings from the dataset and predicted their timber production potential using these methods. I

then calculated the percentage difference between the actual and predicted timber production potential values. For interpolation method 1, the mean percentage difference was 0.58% (standard deviation: 0.39%, maximum: 1.8%); for interpolation method 2, the mean percentage difference was 1.02% (standard deviation: 1.12%, maximum: 5.98%). See Appendix A for further details. These results demonstrate that these techniques are able to use existing data to accurately interpolate between yield curves and find a timber production potential value at alternative planting spacings. The method can therefore be used to derive timber production potential values at a consistent planting spacing, which is an improvement on using different planting spacings for different species.

Carbon

I developed a carbon indicator, which takes into account the cumulative carbon sequestered over time and its subsequent decay. I used data from the Woodland Carbon Code lookup tables [92], which contains the simplified outputs of detailed carbon modelling. For each management option, I included establishment emissions, cumulative carbon sequestration by the forest biomass, ongoing management emissions, clearfell emissions (when appropriate) and wood product decay (both from thinning and clearfell). These separate components are detailed below and represented graphically in Figure 2.4.

Establishment emissions

This included the emissions from growing seedlings in a nursery, fencing, tree shelters, ground preparation and herbicide use. Figures were taken from Table 6 in West and Matthews [92]. A smooth line was drawn between values for different seedling spacings to estimate the value for a spacing of 1.8m, which was not given. Establishment emissions also included loss of carbon from soil disturbance (calculated from tables in West [93]). I assumed planting only occurred on mineral soils, and that the previous land use was woodland. The site preparation closest to that used in Thetford Forest is shallow, plough turfing (double throw mouldboard) so carbon loss from soil disturbance was calculated as -7.34 tCO_2/ha.

Cumulative carbon sequestration

For both continuous-cover and clearfell management options, I used the cumulative biomass sequestration data given in the Woodland Carbon Code lookup tables, and I applied a 20% buffer to account for model precision. The guidance includes maximum sequestration values given for clearfell sites, which are essentially long-term averages of scenarios; these are designed for users who are claiming for carbon sequestration but as I wanted to model the carbon life-cycles of stands I did not use these values. Where thinning took place (after around 20 years, at 5-yearly intervals), I added the value of carbon removed from the forest (taken from the lookup table) to the cumulative carbon total. I then estimated values for each annual interval by deriving a linear relationship

between the value of carbon sequestration after carbon has been removed in thinning and the value of carbon sequestration 5 years later before carbon is removed.

Ongoing management emissions

The emissions resulting from thinning operations.

Clearfell emissions

The emissions resulting from the clearfell process. As indicated in West and Matthews [92], I calculated the clearfell emissions value for each 10-yearly interval by subtracting the cumulative management emissions to that time point from the cumulative management emissions at year 200. This is not shown in Figure 2.4 as clearfell takes place at year 200.

Wood product decay

Wood is sorted into different categories (wood assortment), depending on the type of management and species (Figure 2.5). For conifers, all wood is either saw-log or round wood material; for broadleaves, all wood is either saw-log or goes straight to fuel wood. I used percentage values for wood assortment compositions that are specific to Thetford Forest, developed from conversations with forest managers. During processing at saw mills or processing plants, different products are created and waste produced, which then go to other parts of the processing chain. Carbon values of removal from thinning or clearfells were multiplied by the values in the flow diagram (Figure 2.5) to calculate the total carbon that ends up in different products. For example, if 100t of carbon was removed from the forest in a conifer clearfell, 39.6t would end up as timber products (saw mill wood: $100t \times 72\% = 72t$, timber products: $72t \times 55\% = 39.6t$), 28.672t as board or post products (processed wood: $(72t \times 18\% = 12.96t) + (100t \times 28\% = 28t) = 40.96t$, board/post products: $40.96t \times 70\% = 28.672t$) and 31.728t as fuel products (fuel wood: $(72t \times 27\% = 19.44t) + (40.96t \times 30\% = 12.288t) = 31.728t$, fuel products: $31.728t \times 100\% = 31.728t$).

The different products are then subject to different rates of decay. I used the decay functions outlined in Table 5.7 of Morison et al. [94], shown in Figure 2.5. For timber products and board/post products, this assumes a residence time (60 years for timber and 30 years for board/posts), followed by an exponential decay function (time to reach 5% of the original value is 30 years for timber and 20 years for board/posts). Fuel products have a linear decay lasting 1 year. For the exponential decay functions, I cut off values when they reached less than 1% of the original value.

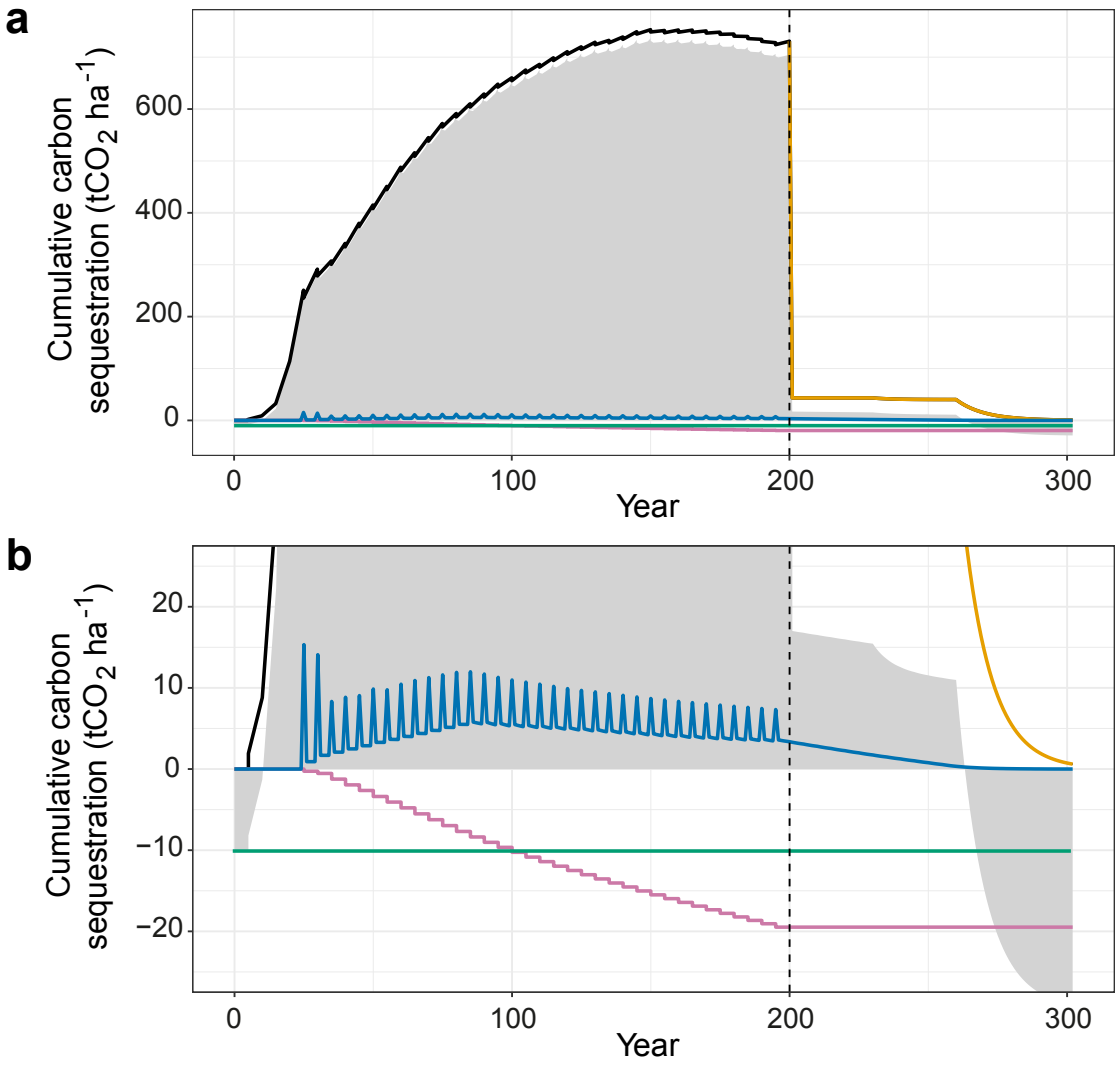

Figure 2.4: Cumulative carbon sequestration for a beech stand (yield class 10, spacing 2.5 m). (a) Full graph, with clearfell at year 200 (dashed vertical line) (b) Same as (a) but zoomed in to focus on x-axis. Black line: cumulative carbon sequestration in living biomass. Orange line: cumulative wood product decay from wood removed in clearfell. Blue line: cumulative wood product decay from wood removed in 5-yearly thinning events. Pink line: cumulative ongoing management emissions (from thinning events). Green line: Establishment emissions. Grey shading: overall cumulative carbon sequestration.

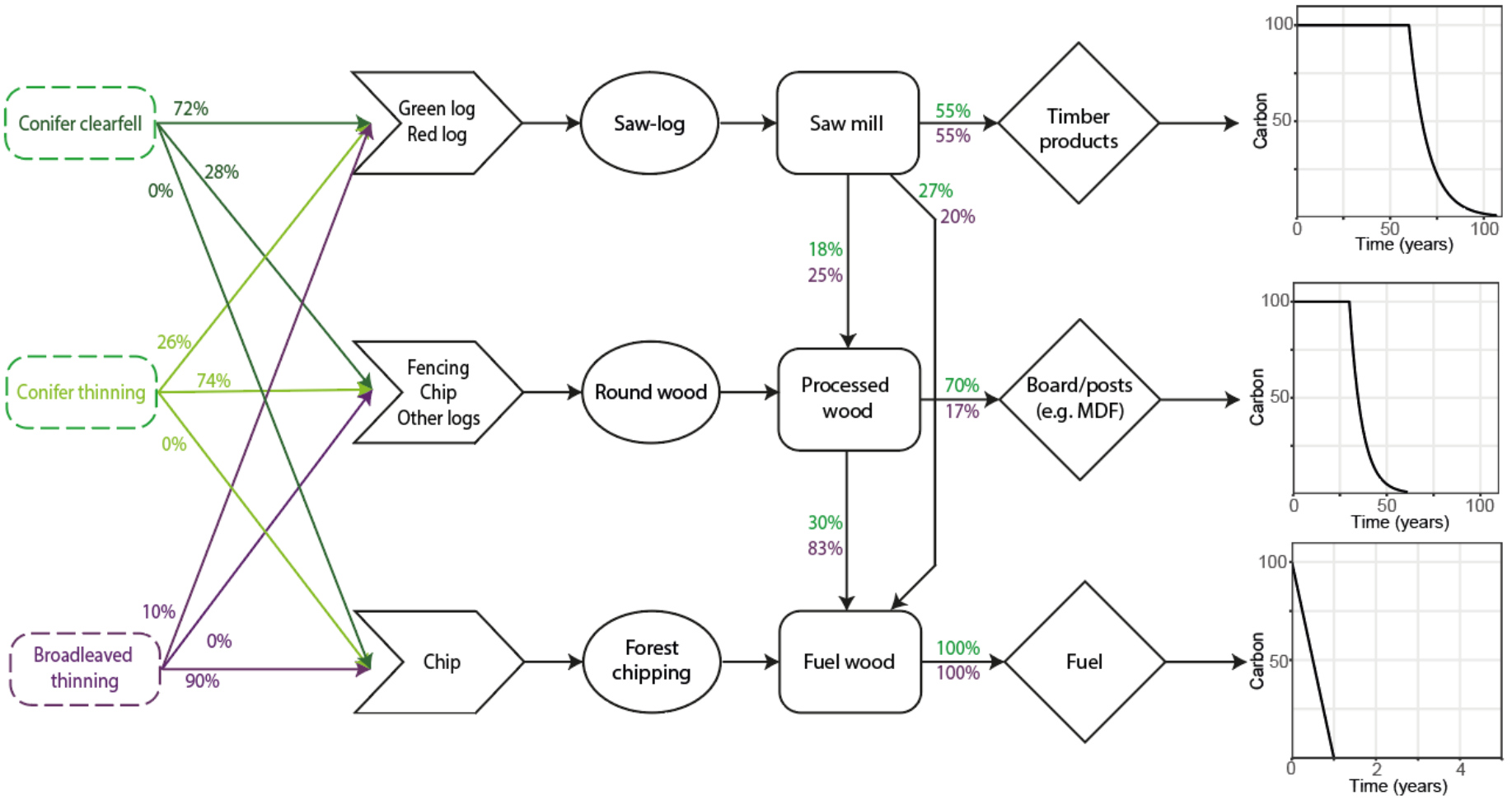

Figure 2.5: Flow diagram showing the stages of harvesting operations, the processing chain and the expected decay of the different wood products. Green values refer to conifers, purple values refer to broadleaves. Adapted from Figures 5.4 and 5.5 and Table 5.6 of Morison et al. [94]

Calculation of carbon indicator

The carbon indicator value for a management option was calculated as the total carbon sequestered, divided by the number of years. The long-term average of a management option (assuming continuous cycling of rotations) will be higher than the short-term value, but management decisions may only be valid for a shorter time period. Therefore, I calculated the carbon indicator for four time periods: 100, 200, 500, 1,000 years. I calculated the total carbon sequestered by adding together the areas under each of the different cumulative curves (emissions curves were assigned a negative value). The four carbon indicators were assessed for each of the management options outlined in Appendix table A.2. For the main analysis, I used the carbon indicator calculated over 200 years, as a long-term but more realistic forestry time horizon. I used a ranking system to determine which management options were most favourable at these different time periods and to calculate whether there were changes in the highest scoring management options.

To further explore the difference in performance of continuous-cover forestry versus clearfell management strategies, I simulated felling years from 40 to 190 years in 10-yearly intervals for Scots pine (yield class 10, spacing 2 m) and calculated the carbon indicators for each time period for each felling year scenario.

Clearfell management options

I assumed that a new rotation was planted 5 years after the clearfell of the previous rotation. During the time period of subsequent rotations, I also accounted for the ongoing decay of wood products (as a result of thinning or clearfell).

Continuous-cover management options

As no detailed models exist for continuous-cover management, I used the available data to model an equivalent management option. Thinning took place at 5-year intervals (from a minimum of around 25 years, depending on tree species). At 40-year intervals, I removed 20% of the oldest trees in the stand. At the same time, I simulated natural regeneration to occupy the cleared 20% (shown schematically in Figure 2.6). After 160 years, there were five different tree groups at different ages, each representing 20% of the total stand area (Figure 2.6). In reality, continuous-cover management options will aim for a more continuous removal and addition of trees, as opposed to 40-year intervals. However, this method approximates the creation of a continuous-cover stand from an even-aged stand.

To calculate the overall cumulative carbon stored over time, the areas under each curve were summed for each time period (as above with clearfell management options). To account for the different percentage compositions of different groups of trees through time, areas under each curve were calculated for each 1-year time period, and then multiplied by their respective percentage composition. Where wood decay from thinning and clearfell events extended into subsequent time periods, they were multiplied by the percentage composition of the original wood product [e.g. 20%

of the oldest component were felled at year 80 but at time of clearfell the oldest component represented 80% of the total area; the carbon removed (and subsequent decay) was therefore multiplied by 16% (80% x 20%)].

Detailed graphical representations of the different components of continuous-cover management options, and the long-term life-cycles of clearfell and continuous-cover management options, are given in Appendix A.

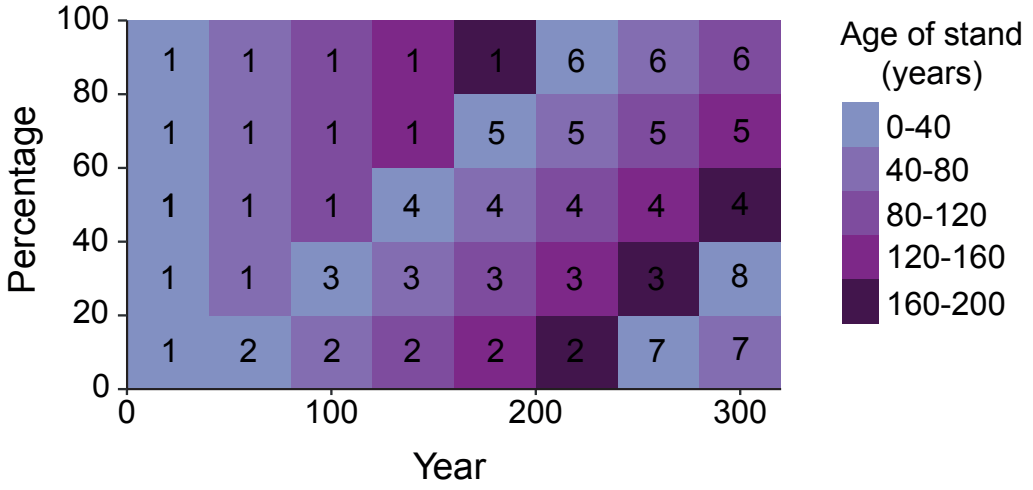

Figure 2.6: Schematic representation of the percentage composition of different stands modelled for continuous-cover. The colour indicates the age of each stand (i.e. trees of the same age). The number in each box corresponds to a stand, and therefore each stand's progression through different age classes. An-even aged stand is established at year 0. 20% of the stand is removed after 40 years, and natural regeneration fills the gap (stand 2). This is repeated every 40 years. After 160 years, the full diversity of ages is represented with each age group representing 20% of the total area.

Mixtures and underplanting

To calculate the carbon indicators of mixtures, I assumed an equal proportion of each species. For clearfell management options, I assumed that the clearfell for all species would take place simultaneously, which I specified as the maximum clearfell age of the different species. I then calculated the carbon indicators separately for each species and calculated the average. To calculate underplanting management options, I assumed that the secondary species was planted 20 years after the first species, and that each species was felled at its optimal time, so clearfells took place separately for each species. Subsequent rotations of the first species were planted 5 years after the felling of the second species from the previous rotation. I assumed an equal proportion of each species, so multiplied each by 0.5.

Specifying the table to use from the lookup tables

Only a subset of planting spacings and yield classes are provided for a selection of species in the carbon lookup tables. When a species was not provided, I used the species that most closely

represented it, as detailed in Appendices 1 and 2 in the carbon lookup guidance [92]. The sycamore/ash *Fraxinus excelsior*/birch *Betula spp.* thinned management option does not have complete data, so I used the tables for oak *Quercus spp.* instead. I estimated the yield class that most approximated the sycamore/ash/birch management option by comparing unthinned data. I used the spacing available for each species that was closest to 2 m, which is the spacing most applicable to Thetford Forest management. I specified the age of clearfell as when the mean diameter breast height of the tree was 40 cm, which is the ideal size to harvest, to the closest 10-yearly interval. I used the available timber yield models to estimate this age, using the specified equivalent species table if the species was not available. I set a cut-off age at 80 years. See Table 2.1 for full details.

Assumptions of the carbon modelling

I assumed that the carbon removed from the forest (provided in the lookup tables) was equivalent to the carbon that is taken from the standing biomass. I used this value to calculate the 'teeth' in the cumulative carbon curve at each thinning event. This is likely to be an underestimate, as some carbon may be removed from the standing carbon but remain within the forest (for example, as woody debris).

All planting spacings were not available for all species, so I had to use the spacing that was closest to 2 m, which is not ideal. However, the carbon accumulated at different spacings tends to converge over time as more widely spaced trees tend to be grow bigger, and vice versa. Additionally, thinning events account for planting spacing. Similarly, I was unable to account for the difference in planting spacings that might occur in mixtures and underplanting management options, i.e. trees of the same species would on average be more widely spaced than in a monoculture stand. However, the spacing accounts for growth rates of trees given crowding by other trees, which will be similar regardless of tree species, so it is still appropriate to use a lower planting spacing. It was potentially more problematic when species in mixtures were not available at the same spacings, but unavoidable.

Planting spacings also alter the optimal clearfell age (the age at which trees approximate 40 cm diameter breast height). The clearfell age used in these calculations for some species therefore differed from the reality in Thetford Forest, as the 2 m spacing was not available. However, the carbon accumulated should be roughly equivalent as the trees reach the same diameter breast height.

Finally, when modelling continuous-cover management options, I assumed that removing 20% of carbon from the oldest trees would free up 20% of the area for new planting. This may be an overestimate of the area as larger trees store more carbon than smaller trees. However, the area around larger trees will be greater due to previous thinning events. It is difficult to predict exactly how these models therefore might translate in a real continuous-cover stand.

Yield classes

For both timber and carbon, I used the detailed subcompartment database from Thetford Forest to find the average yield class of different species (separately when species were in monocultures and mixture), weighted by the area of each type of yield class across the forest. I rounded the average to the nearest even number (yield classes are only in even numbers). If the even number was below the minimum yield class for which data exists, by one or two categories, I rounded the yield class up; otherwise I excluded the species. Where a species did not have its own yield table or carbon calculations, I used an appropriate alternative species, as recommended in the associated guidance. This information is given in Table 2.1.

Deer

Thetford Forest has high densities of native roe deer *Capreolus capreolus* and red deer *Cervus elaphus*, and non-native fallow deer *Dama dama* and muntjac *Muntiacus reevesi* [68]. To determine whether deer have different impacts on different forested management options, I incorporated costs of their damage and management and income from venison and hunting. There are no data on the cultural value of deer in Thetford Forest, so this benefit was excluded from the analysis. To assess the overall impacts of deer, I calculated a cost-benefit analysis for each management option:

$$D = V + DCL + S - C - F - R$$

where,

D = Deer impact to management option

V = Venison income

DCL = Deer control licence income

S = Permit stalking income

C = Crop replacement costs

F = Fencing costs

R = Ranger costs

Venison income, deer control licence income, fencing costs and ranger costs were calculated as a forest-wide average. The costs of crop damage to a management option were calculated on a per hectare basis; I therefore multiplied this by the total area of the forest (18731.11 ha) to allow comparisons to other figures and incorporate this into the total estimate. Where values were calculated as means, I randomly sampled the distribution of these values (a truncated normal distribution above 0) and added together the different components. I repeated this 10,000 times to calculate an overall mean and standard deviation for D.

*Table 2.1: Species information. Blue highlighting indicates conifers, yellow highlighting indicates broadleaves. Darker highlighting indicates species that are assessed as individual monocultures. Lighter highlighting indicates species that are grouped together into 'other conifer' or 'other broadleaved' monoculture options. *Japanese cedar is not assessed as a monoculture, only in mixture.*

Species		Lookup species (if different)		Spacing	Monoculture			Mixture		
					Yield class		Fell age (carbon)	Yield class		Fell age (carbon)
Common name	**Scientific name**	**Timber**	**Carbon**		**Average**	**Used**		**Average**	**Used**	
Corsican pine	*Pinus nigra*			1.4	14.35	14	60			
Douglas fir	*Pseudotsuga menziesii*			1.7	12.35	12	70	12.54	12	70
Hybrid larch	*Larix × marschlinsii*	Japanese larch		1.7	10.08	10	80	9.9	10	80
Japanese larch	*Larix kaempferi*			1.7	9.53	10	80			
Scots pine	*Pinus sylvestris*			2	10.64	10	70	10.58	10	70
Serbian spruce	*Picea omorika*	Norway spruce		1.5	8.49	8	80	10.25	10	80
Western hemlock	*Tsuga heterophylla*			1.5	16	16	80	12.26	12	80
Western red cedar	*Thuja plicata*			1.5	14	14	80	11.22	12	80
Japanese cedar*	*Cryptomeria japonica*	Western red cedar		1.5			80	12.26	12	80
Atlas cedar	*Cedrus atlantica*	Scots pine	Noble fir	1.5	9.62	10	80			
European larch	*Larix decidua*			1.7	9.77	10	70			
European silver fir	*Abies alba*	Noble fir		1.5	12	12	80			
Grand fir	*Abies grandis*			1.8	15.49	16	80			
Lawsons cypress	*Chamaecyparis lawsoniana*	Western red cedar		1.5	11.23	12	80			
Leyland cypress	*× Cuprocyparis leylandii*	Western red cedar		1.5	10.77	12	80			
Lodgepole pine	*Pinus contorta*			1.5	10	10	80			
Macedonian pine	*Pinus peuce*	Corsican pine		1.4	10.41	10	80			
Maritime pine	*Pinus pinaster*	Lodgepole pine		1.5	10	10	80			
Noble fir	*Abies procera*			1.5	14	14	80			
Norway spruce	*Picea abies*			1.5	11.2	12	80			
Other conifers		Norway spruce		1.5	16	16	60			
Ponderosa pine	*Pinus ponderosa*	Scots pine		2	10	10	70			
Sitka spruce	*Picea sitchensis*			2	14	14	60			

Wellingtonia	*Sequoiadendron giganteum*	Grand fir		1.8	8.71	12	80			
Weymouth pine	*Pinus strobus*	Scots pine		2	11.21	12	60			
Birch	*Betula spp.*	Sycamore	Oak	2.5	3.75	4	N/A	4.2	4	
Eucalyptus	*Eucalyptus spp.*	Poplar	Oak	2.5	11.22	8	N/A			
Sweet chestnut	*Castanea sativa*	Beech		2.5	2.1	4	N/A	4.38	4	
Alder	*Alnus spp.*	Sycamore	Oak	2.5	2.63	4	N/A			
Ash	*Fraxinus excelsior*	Sycamore	Oak	2.5	3.84	4	N/A			
Aspen	*Populus tremula*	Poplar	Oak	2.5	6	4	N/A			
Beech	*Fagus sylvatica*			2.5	5.67	6	N/A	6.17	6	
Black walnut	*Juglans nigra*	Oak		2.5	4	4	N/A			
Common alder	*Alnus glutinosa*	Sycamore	Oak	2.5	6	4	N/A			
Elm	*Ulmus spp.*	Beech		2.5	2.79	4	N/A			
Hornbeam	*Carpinus betulus*	Beech		2.5	5	6	N/A			
Italian alder	*Alnus cordata*	Sycamore	Oak	2.5	4	4	N/A			
Lime	*Tilia spp.*	Sycamore	Oak	2.5	3.2	4	N/A			
Norway maple	*Acer platanoides*	Sycamore	Oak	2.5	4.2	4	N/A			
Oak	*Quercus spp.*			2.5	4.22	4	N/A	4.11	4	
Other broadleaves		Sycamore	Oak	2.5	2	4	N/A			
Poplar	*Populus spp.*		Oak	2.5	5.88	4	N/A			
Raoul	*Nothofagus nervosa*	Roble	Oak	2.5	6	4	N/A			
Red oak	*Quercus rubra*	Beech		2.5	4	4	N/A			
Sycamore	*Acer pseudoplatanus*	Sycamore	Oak	2.5	3.68	4	N/A	4.84	4	
Tulip tree	*Liriodendron tulipifera*	Poplar	Beech	2.5	2	4	N/A			

Venison income

Data on the number of carcasses killed and sale prices per carcass were available from 2012-2017. I aggregated the total income across the forest for each year and calculated the mean and standard deviation across years.

Deer control licence and permit stalking income

Some areas of Thetford Forest are managed under a deer control licence, whereby rights to shoot are sold to other parties. Similarly, stalking is sold to private individuals, who can stalk deer in the forest under supervision of one of the wildlife rangers. I therefore calculated the total annual income from these two incomes.

Crop replacement costs

I used data from beat-up* surveys carried out across the forest to estimate the annual cost of replacing crops as a result of deer damage. Newly planted crops are visited after the first year to assess whether any of the crop has been killed through mammal browsing, primarily by deer and rabbits. If damage has occurred, the percentage of the crop killed is estimated through transect sampling (one in 5 rows where sites are under three hectares; one in ten rows where sites are greater than three hectares). I categorised the visited compartments by management option and analysed the effects of management option on total damage through an ANOVA and Tukey-Kramer pairwise comparisons test. Beat-up surveys from the 2015 and 2016 planting seasons were analysed.

For each management option, crop replacement is $B + R$, where B is beat-up cost and R is restock cost:

$$B = L_b \times C_b$$
$$R = L_r \times C_r$$

where,

L = likelihood of a management option needing to be beat-up (L_b) or of failing completely (L_r).

C = average cost of replanting for beat-ups (C_b) or restocks (C_r)

Likelihood of a management option needing to be beat-up (L_b) was calculated from previous years' data on the number of subcompartments that were planted and those that received replanting. Beat-ups can happen to subcompartments that were planted over the previous five planting seasons. The number of subcompartments that actually received beat-ups for each management option was

* Beat-up is the forestry term used when newly planted crops are supplemented with additional new planting in consecutive years, for example as a result of herbivore damage or establishment failure. It is distinct from restocking, when either the entire crop fails to establish and needs to be replaced or following a felling operation.

calculated as a percentage of the number of 'potential' subcompartments, i.e. been planted in the previous five years. This was calculated for three over-wintering planting seasons (covering 2013 – 2016).

Likelihood of a management option needing to be restocked due to complete crop failure (L_r) was calculated from the beat-up surveys. The number of sites with 100% crop damage were classified as failures. L_r is expressed as a percentage of the total number of sites surveyed for each management option. Survey data from two planting seasons were available.

The average costs for beat-ups and restocking were calculated from historical data on replanting (3 over-wintering planting seasons covering 2013-2016). Records indicate the number of trees allocated to compartments for either beat-ups or restocking, and the associated individual tree and delivery costs. Where a batch of trees was assigned to more than one subcompartment, I divided the number of trees between sites based on area. In addition, I incorporated a flat rate of planting by contractors (£200 per 1,000 trees planted) to find a total cost of beat-up or replanting for each subcompartment site. Finally, I divided total cost by area to find a cost per hectare. Each site was classified into a management option and the per hectare costs averaged for each management option. I calculated the mean cost over all years.

To find a total crop replacement cost, I took the mean and standard deviation of the log-transformed raw data of beatup and restock costs (data was right-skewed so a log distribution brought the data closer to a normal distribution). I then randomly sampled the normal distribution (truncated above 0) using these means and standard deviations 10,000 times and took the exponential to convert them back to observed values. These cost values were multiplied by their respective likelihood values to find sets of B and R values. B and R values were then paired and added together to find a set of 10,000 total crop replacement values. As this was a per hectare cost, I then multiplied each value by 18,731.11 to get a whole forest final value. I calculated a mean and standard deviation of these final values, repeating the process for each management option.

In my calculations for likelihoods and costs of beat-ups or restocks, I only analysed management options that had at least 15 records across these categories. No broadleaved management option had sufficient data, so I amalgamated broadleaves into one category. This included data from birch monoculture, sweet chestnut *Castanea sativa* monoculture, eucalyptus *Eucalyptus spp.* monoculture, other broadleaved monoculture, and broadleaved mixtures. Similarly, conifer and broadleaved mixtures (where the primary component was broadleaved) did not have sufficient samples sizes across all categories, so conifer and broadleaved mixtures (where the primary component was broadleaved or conifer) were also amalgamated.

Fencing

Fencing is erected to protect crops from mammal damage. The decision on whether to fence a new planting area considers a multitude of factors, such as ranger opinion, boundary proximity, soil type and recreational and public access. Therefore, the cost of fencing was considered separately to the choice of management option. Detailed invoices were available for the over-wintering planting seasons covering 2014 – 2016. I calculated the average cost per metre of deer fencing (including material, gates and erection costs). This was used to estimate a per-year fencing cost, based on the metres of fencing erected, and a yearly average (2012-2016). The estimate included only fencing for deer. Fencing to protect crops against rabbits also takes place across the forest (average cost £32,025.95 per year).

Ranger costs

I calculated the total annual cost of a wildlife ranger, which includes salary, allowances and vehicle costs. This was multiplied by the total number of wildlife rangers operating across the forest (five). The total excludes the costs of the wildlife manager.

Comparison across all ecosystem services

To compare the results of timber, carbon and deer for each management option, I scaled the calculated values between 0 and 1:

$$\tilde{x} = \frac{x}{\max_x}$$

where,

$\tilde{x}$ = the scaled value

x = the raw ecosystem service value,

$\max_x$ = the maximum value of all the raw ecosystem service values.

Where deer values were not calculated for a particular management option and ecosystem service combination due to lack of data, the closest alternative was used; for example, the value for other conifer monoculture was used for western hemlock *Tsuga heterophylla* monoculture.

I then added the scaled values together (using the continuous-cover management strategy for carbon) across the three ecosystem services for each management option to find a total scaled value.

RESULTS

Timber

Of the conifer monoculture options, western hemlock had the highest timber production potential (16.0), followed by western red cedar (14.0) and Corsican pine (13.96) (Figure 2.7a). Serbian spruce *Picea omorika* had clearly the lowest timber production potential of the conifer monoculture options. All conifer mixtures were very similar, with values of between 11.0 and 11.6, with the

exception of Serbian spruce as a secondary species in a two-species mixture (Scots pine pioneer: 9.4, hybrid larch *Larix* × *marschlinsii* pioneer: 9.5) (Figure 2.7b and Figure 2.7c). For conifer mixtures, a hybrid larch pioneer performed slightly better than a Scots pine pioneer.

Eucalyptus had the greatest timber production potential (26.0), with a value more than double any other option except western hemlock, western red cedar or Corsican pine monoculture (Figure 2.7e). Birch and sweet chestnut monoculture, and the broadleaved mixture options, all had relatively low values (3.9-4.6) (Figure 2.7e and Figure 2.7f). For the conifer and broadleaved mixture options, beech *Fagus sylvatica* and Scots pine outperformed oak and Scots pine mixture (Figure 2.7d). Overall, all conifer options were better than the broadleaved options, with the exception of eucalyptus. The conifer and broadleaved options were better than Serbian spruce monoculture, although otherwise between conifer and broadleaves.

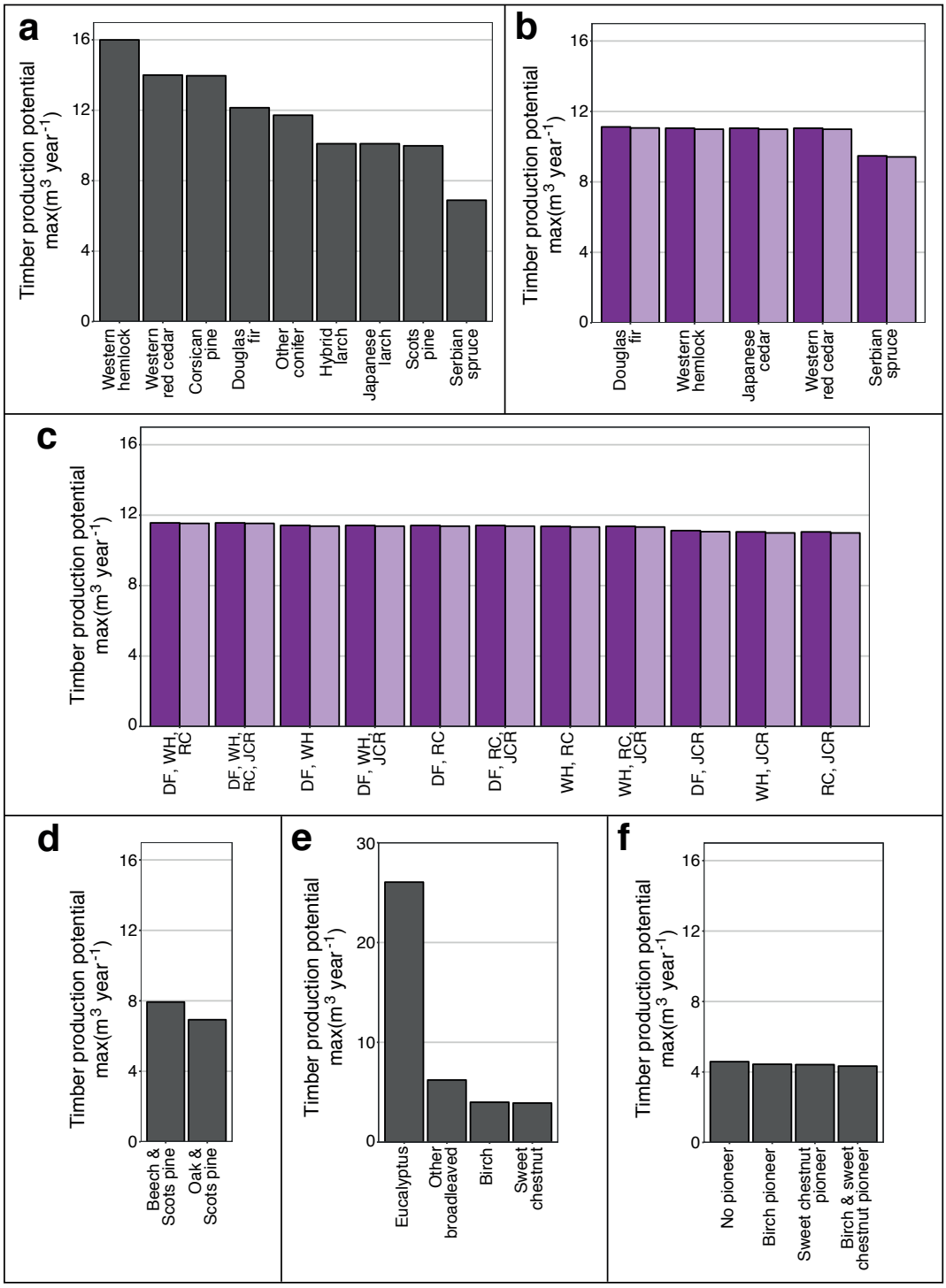

Figure 2.7: Timber production potential of different management options. Timber production potential is calculated as the maximum value of timber production divided by year [max($m^3 year^{-1}$)]. All graphs are presented on the same y-axis scale, except for part (e), which has a longer scale. Bars are ordered by decreasing timber production potential. (a) Conifer monocultures. (b) Conifer mixtures (maximum two species). The first species in the mixture is indicated by the bar colour (dark purple: hybrid larch pioneer, light purple: Scots pine pioneer). The second species is indicated by the x-axis label. (c) Conifer mixtures (more than two species). The first species in the mixture is indicated by the bar colour [as for part (b)]. The secondary species are indicated by the x-axis labels. Species are given as symbols for clarity, as follows. DF: Douglas fir, WH: western hemlock, RC: western red cedar, JCR: Japanese cedar. (d) Conifer and broadleaved mixtures. (e) Broadleaved monocultures. (f) Broadleaved mixtures. The x-axis label indicates the pioneer species in addition to the mixture of beech, oak and sycamore.

Carbon

When evaluated over a 200-year time period, continuous-cover was universally higher performing for all management options that were assessed under both continuous-cover forestry and clearfell strategies (Figure 2.8a and Figure 2.8b). The average relative carbon indicator value of clearfell compared to continuous-cover strategies was 87.7% for conifer monocultures and 81.1% for conifer mixtures. When assessed under clearfell, rather than continuous-cover strategies, the order of the best conifer monoculture options slightly differed, with Douglas fir *Pseudotsuga menziesii* and Corsican pine ranking higher compared to the continuous-cover order. Western hemlock was the best performing conifer monoculture option, under both continuous-cover and clearfell strategies. Japanese larch *Larix kaempferi*, hybrid larch and Serbian spruce had the lowest carbon indicators for the conifer monoculture options under both strategies and had roughly the same continuous-cover carbon indicator values as the broadleaved monocultures of other broadleaved or birch. Eucalyptus was the highest performing broadleaved monoculture option, outperforming Corsican pine, Scots pine, Japanese larch, hybrid larch and Serbian spruce monocultures.

As for the conifer monocultures, continuous-cover was better than clearfell strategies for conifer mixtures (Figure 2.8b). Furthermore, underplanting had lower carbon indicator values than simple mixtures without a planting delay for the second species component. The Scots pine pioneer options also universally outperformed the hybrid larch pioneer options, as would be expected given that Scots pine monoculture had higher carbon indicator values than hybrid larch monoculture. Mixtures with Douglas fir as the second species had the highest value of each of the different categories.

Interestingly, all types of broadleaved mixture had higher carbon indicator values than all the broadleaved monoculture options except eucalyptus (Figure 2.8c). The option without a pioneer was the best broadleaved mixture option for carbon. Conifer and broadleaved mixtures were even better, with values that exceeded Japanese larch, hybrid larch or Serbian spruce managed as either continuous-cover or clearfell, or Scots pine managed as clearfell (Figure 2.8d).

The full results for all carbon indicators are given in Appendix table A.3.

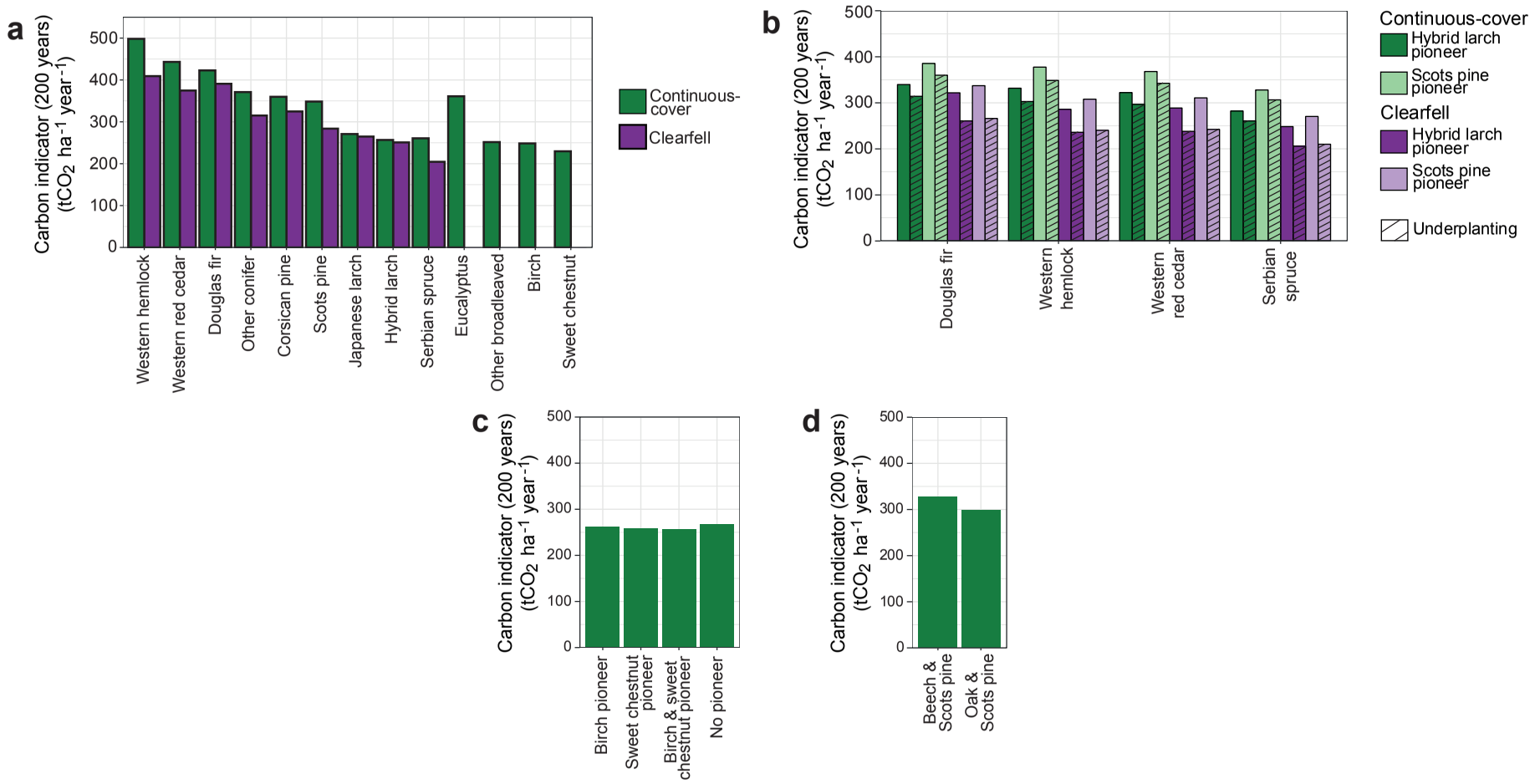

Figure 2.8: Carbon indicator values for management options measured over a 200-year time period. Green bars indicate values for continuous-cover management, purple bars indicate values for clearfell management. (a) Monocultures. Broadleaved species are only measured under continuous-cover management. Bars are ordered by the value of continuous-cover strategies, with broadleaves after conifers. (b) Conifer mixtures (maximum of 2 species). The first species in the mixture is indicated by the bar colour, the second species is indicated by the x-axis label. (c) Broadleaved mixtures. The x-axis label indicates the pioneer species in addition to the mixture of beech, oak and sycamore. (d) Conifer and broadleaved mixtures.

For clearfell management options, the carbon indicator value increased as fell year increased (Figure 2.9). When measured over short time scales (100 or 200 years), clearfell management options with a long fell time performed better for carbon than continuous-cover management options. For example, Scots pine (yield class 10, spacing 2 m) felled at year 90, or after, performed better than continuous-cover when measured over a 100-year period, or felled at year 170 or after when measured over a 200-year period. However, when measured over longer periods, continuous-cover always performed better. The reasons for these differences are illustrated in Figure 2.10, where the carbon indicator value is represented as the area under each curve. When measured over 100 years, clearfell management with a fell year of 190 sequestered more carbon than continuous-cover management, where 20% of the largest carbon is removed from every 40 years. However, clearfell management with a fell year of 70 performed more poorly than continuous-cover due to

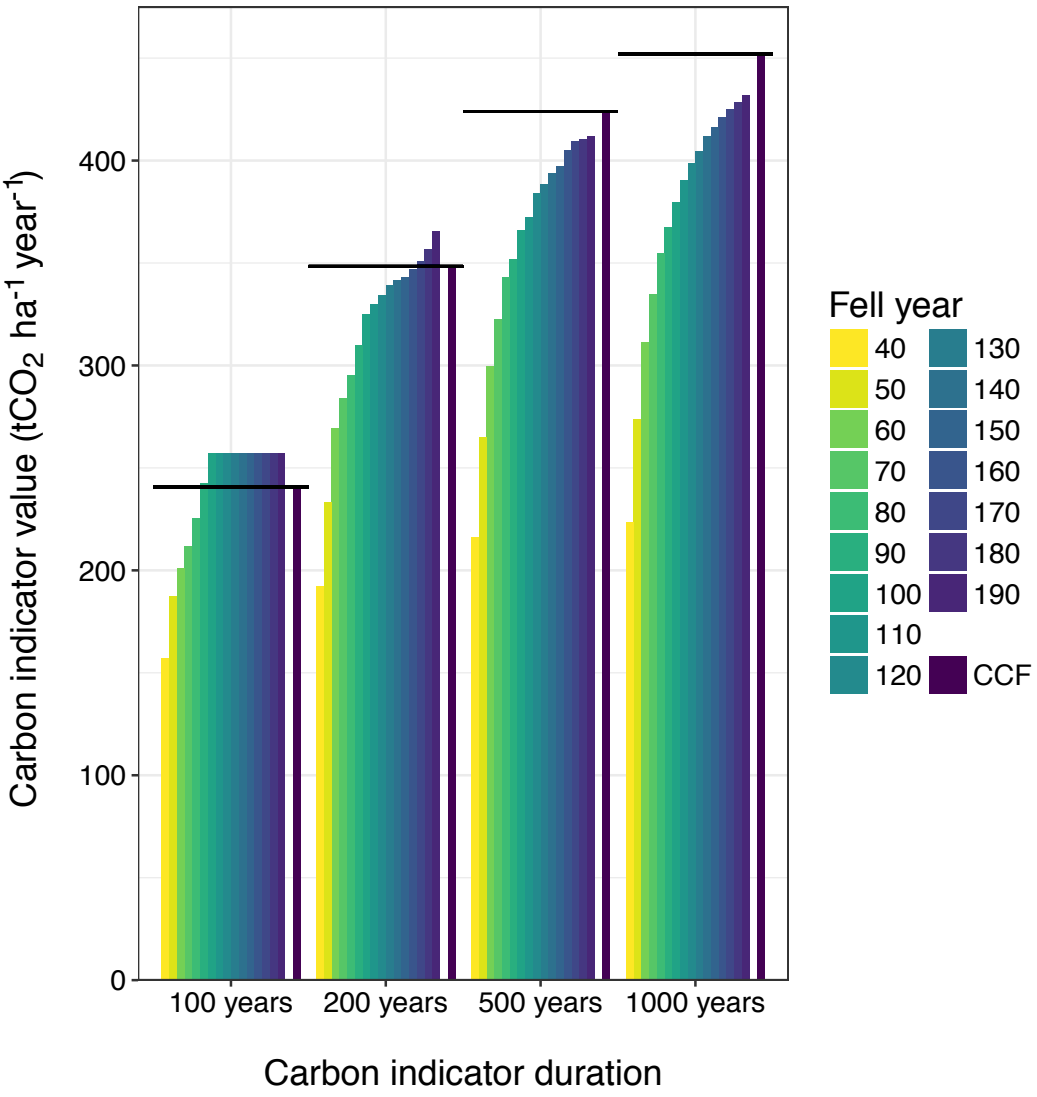

Figure 2.9: Carbon indicator values for Scots pine (yield class 10, spacing 2 m) with different management strategies when measured over different time periods. Fell year indicates the felling age of stands managed under clearfell rotations. CCF indicates the reference value of the same stand managed under continuous-cover.

the rapid loss of carbon after felling (in decay of wood products). When measured over 200 years, felling at year 190 still performed slightly better than continuous-cover management; however, when measured over 500 years, continuous-cover performed better because the overall cumulative carbon had a higher average value and did not fluctuate as dramatically as any clearfell system.

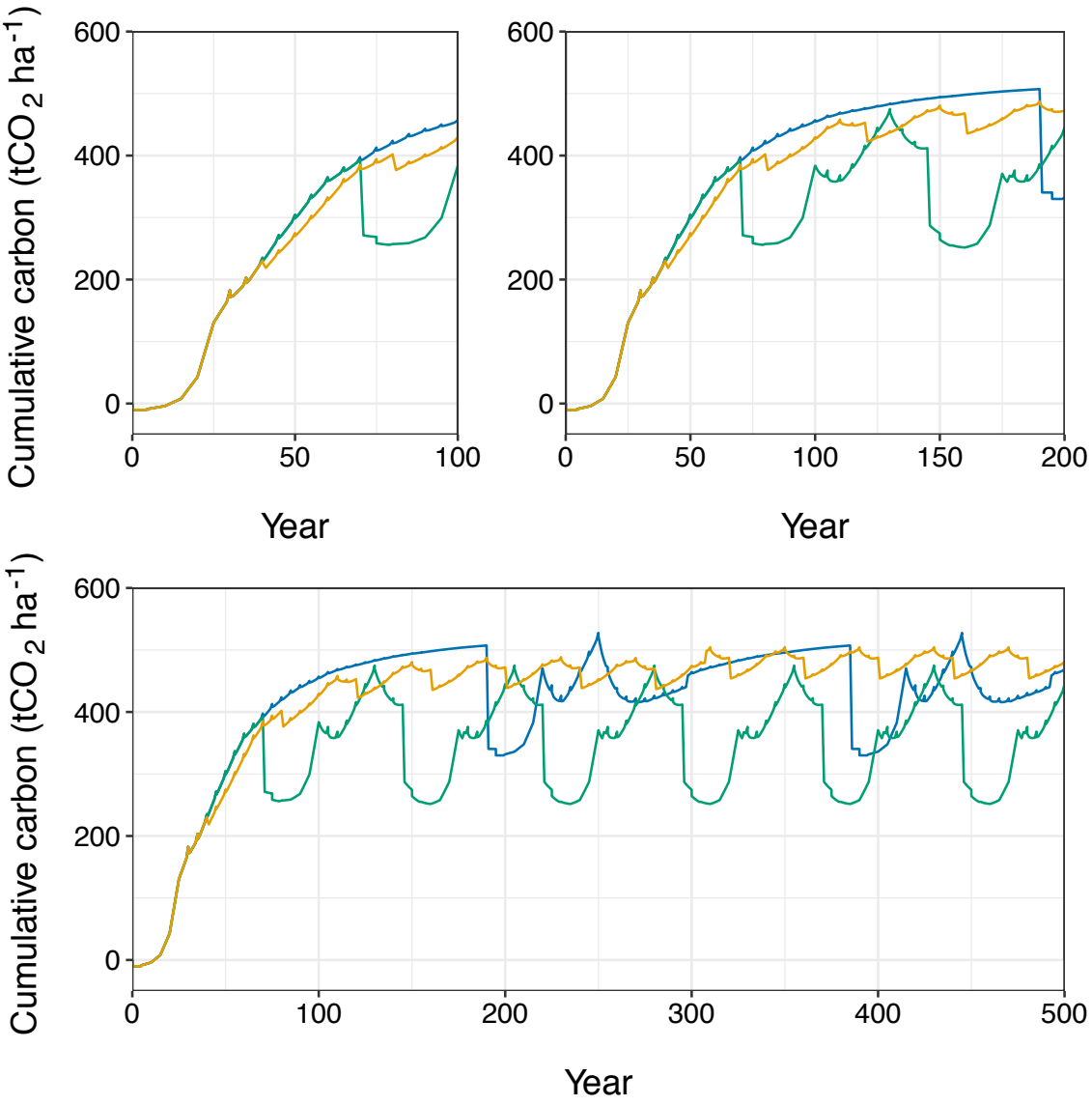

Figure 2.10: Total cumulative carbon sequestration for Scots pine (yield class 10, spacing 2 m) with different management strategies. Different panels show different total time periods (100, 200 and 500 years respectively). Green lines indicate clearfell management with a fell year of 70, blue lines indicate clearfell management with a fell year of 190. Yellow lines indicate continuous-cover management.

When the carbon indicator was calculated over different time-scales the ranking of management options changed (Figure 2.11 and Figure 2.12). The absolute values of the carbon indicator increased, and there were greater differences between management options. The greatest changes in ranks were between 100 and 200 years; there was relatively little difference between 500 and 1000 years. Generally, as the duration of measurement increased, conifer monoculture clearfell options decreased in rank, whereas conifer monoculture continuous-cover options increased in rank, although there were exceptions to this (Figure 2.11b). There was a very clear trend for conifer mixtures: whereas clearfell and continuous-cover management strategies were fairly mixed in rank order when the carbon indicator was calculated over 100 years, there was increasing differentiation between the two management strategies as the duration of measurement increased (Figure 2.12b). By 1,000 years, continuous-cover strategies occupied the top 10 ranks and clearfell strategies occupied the bottom 10 ranks. In particular, continuous-cover with a Scots pine pioneer was particularly dominant, with the top ranks occupied exclusively by these options by year 500. This was mirrored in results for conifer mixtures that had more than two species, when all Scots pine pioneer mixture options outperformed all hybrid larch pioneer mixture options by year 200 (Appendix figure A.16). In contrast, there was no change in the ranks of either broadleaved mixtures or conifer and broadleaved mixtures as the duration of measurement increased (with the exception of between 100 and 200 years for broadleaved mixtures, when the sweet chestnut pioneer option swapped with the birch and sweet chestnut pioneer option).

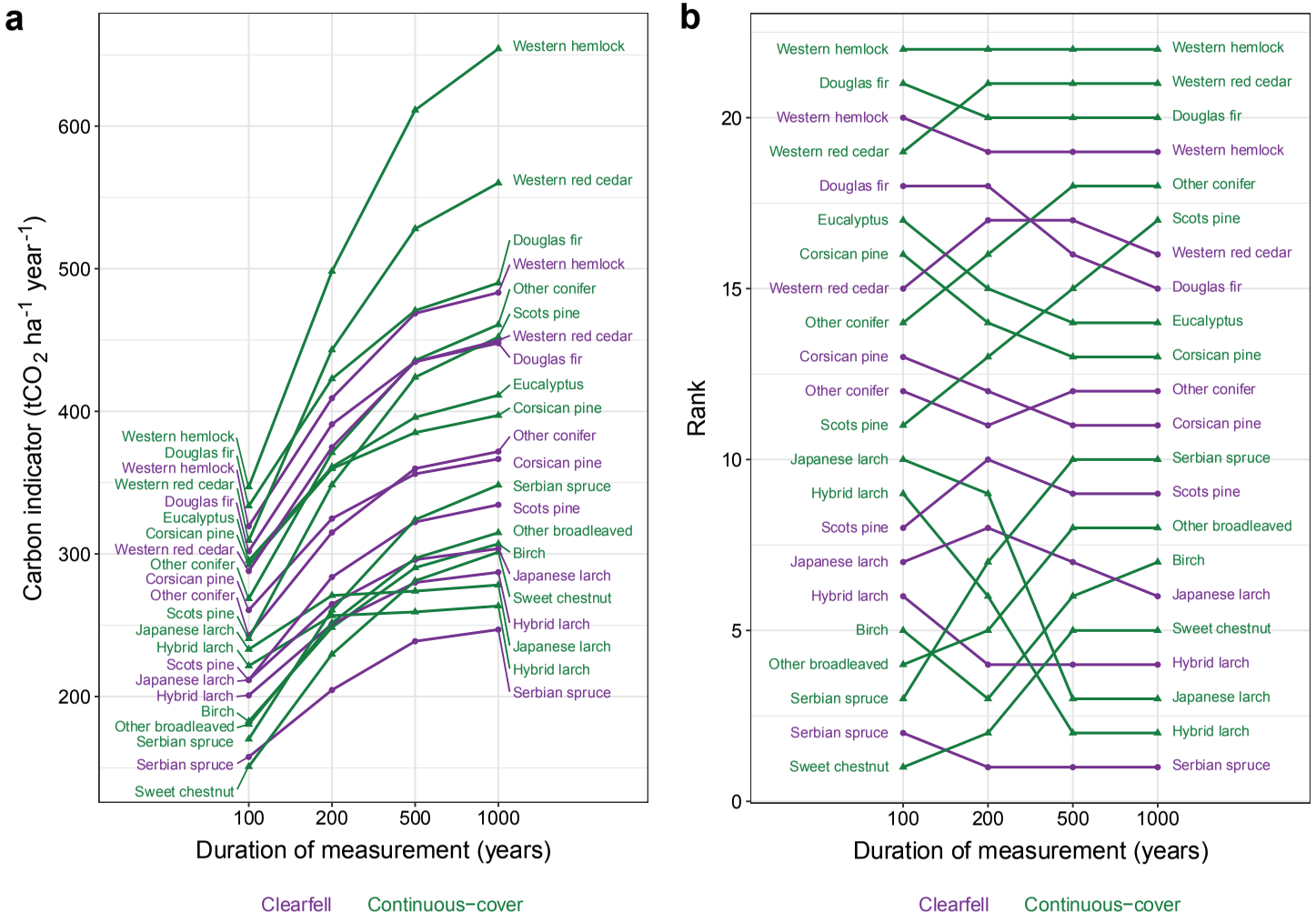

Figure 2.11: The change in the orders of species monocultures depending on the duration of measurement for the carbon indicator. The colour indicates whether the monoculture is managed as clearfell or continuous-cover. (a) The absolute values of the carbon indicator. (b) The relative rank of different options. Higher rank value indicates higher carbon indicator value.

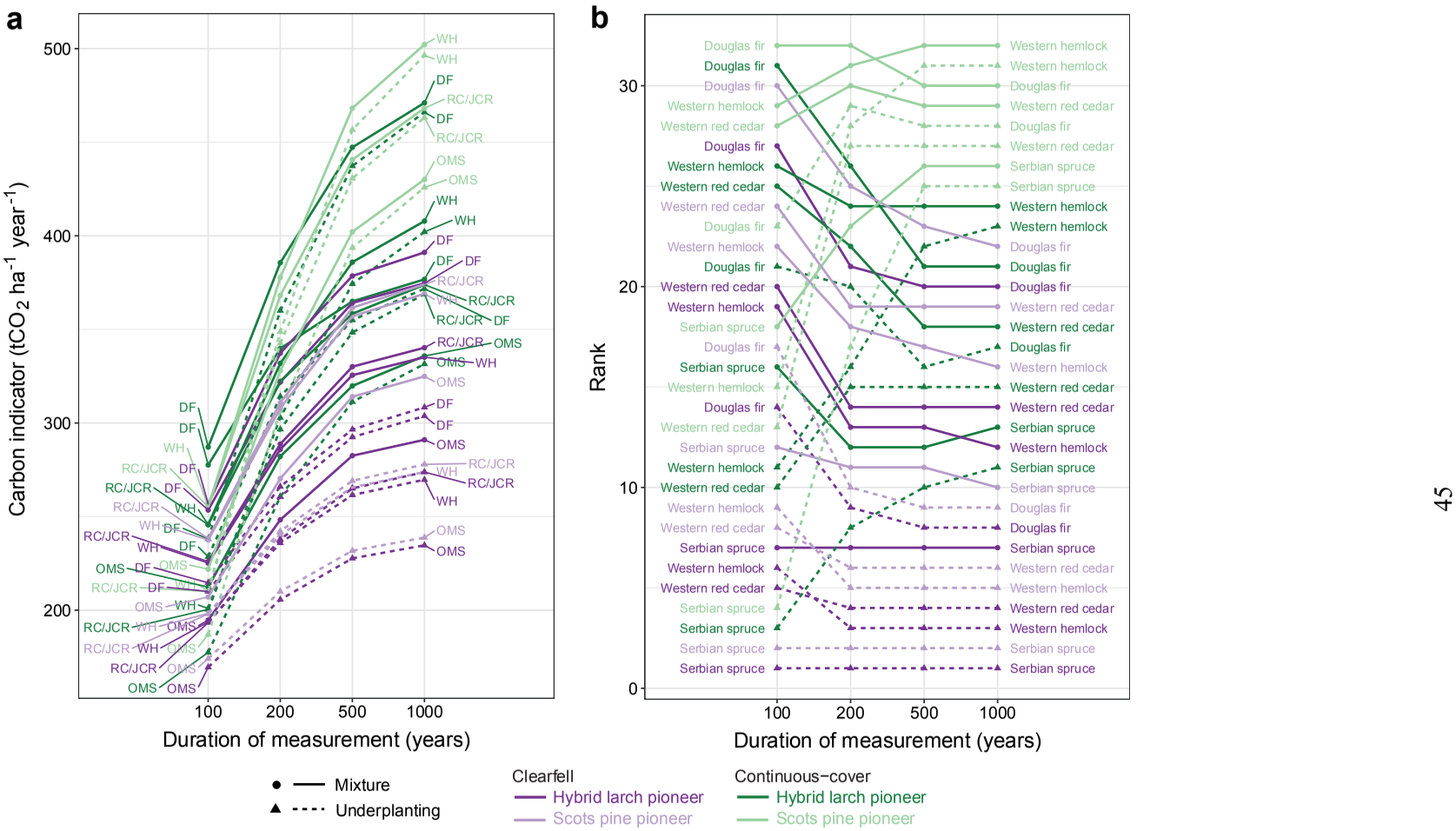

Figure 2.12: Change in the orders of conifer mixtures according to the duration of measurement. The colour indicates whether the mixture is managed as clearfell or continuous-cover, and the shading indicates the pioneer species. The line type and symbol indicates whether the mixture is managed as a pure mixture of equal ages or using underplanting. (a) The absolute values of the carbon indicator. Species are given as symbols for clarity, as follows. WH: western hemlock, DF: Douglas fir, RC: western red cedar, OMS: Serbian spruce. (b) The relative rank of different options. Higher rank value indicates higher carbon indicator value.

Deer

Management option was a significant predictor of total browsing damage ($P = 1.10\text{x}10^{-4}$, Figure 2.13a). There was generally high variation in the data, and each management option recorded at least one failure (100% damage) due to browsing. Scots pine monoculture and conifer and broadleaved mixture had the lowest average damage; according to the Tukey-Kramer pairwise comparisons, both were significantly lower than other conifer monoculture and the broadleaved management option, which had the highest average damage. Given that management option significantly affected total browsing damage, it was appropriate to continue to analyse costs from deer damage for different management options.

Damage to a crop does not necessarily result in beat-up plantings, so the likelihood of beat-ups was calculated from actual replanting data. All management options except other conifer monoculture and broadleaved were more likely to have beat-up replantings than restocks (Figure 2.13b). The greatest beat-up likelihood was for larch monoculture (26.5%) and at least 10% of all types of conifer monoculture had beat-up replantings. In contrast, broadleaved had a very low beat-up likelihood (2.1%) but the highest restock likelihood (33.3%).

The average costs to restock or beat-up were fairly similar across different management options (with the exception of other conifer monoculture) and there was high overall variation (Figure 2.13c). Conifer and broadleaved mixture had the lowest average beat-up cost (£15.20 per ha) and larch monoculture had the lowest average restock cost (£72.84 per ha). The highest average restock cost was for other conifer monoculture (£148.36 per ha), which was more than 1.5 times higher than the next highest option: conifer mixture.

For the total replanting cost (Figure 2.13d), conifer and broadleaved mixture has the lowest mean value, reflecting its relatively low beat-up and restock likelihoods and low average beat-up cost (Figure 2.13b and Figure 2.13c). Other conifer monoculture had the highest mean total replanting cost, reflecting the high restock likelihood and restock cost. The highest mean total replanting cost (other conifer monoculture) was over seven times greater than the lowest cost (conifer and broadleaved mixture). Nevertheless, there was high overall variation in total costs for each management option, and standard deviation increased as the mean increased.

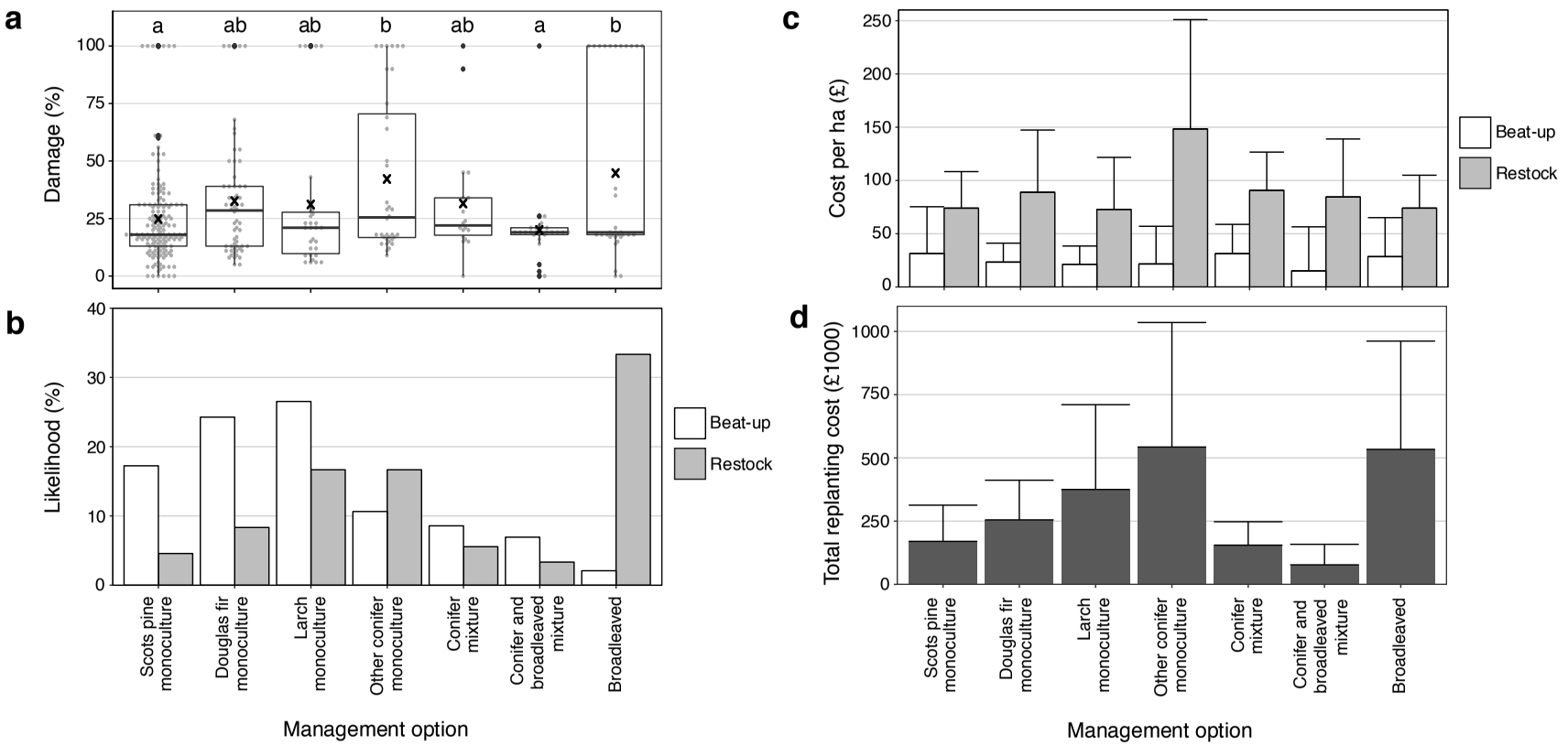

Figure 2.13: Deer damage effects on different management options. (a) The percentage of crop measured as damaged in the beat-up surveys (2014-2016). Grey points indicate empirical data, black crosses indicate the means. Boxplots with different letters indicate significant pairwise differences between management options (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different, at P = 0.05. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Black points indicate values that are beyond the whiskers. (b) The likelihood of a beat-up or restock. Beat-up likelihood is expressed as the percentage of eligible subcompartments (i.e. those planted within the last five years) that received beat-up planting. Restock likelihood is expressed as the percentage of subcompartments that were classified as failures (100% crop damage) in the beat-up surveys. (c) The average cost of beat-up or restock plantings. Bars indicate the mean values and error bars indicate the standard deviation. (d) The average total replanting cost. Bars indicate the mean values and error bars indicate the standard deviation.

The calculated values for all the components of the total deer cost, except the crop replacement costs, are detailed in Table 2.2. The annual ranger cost was more than twice the income generated from venison (as a by-product of culls), deer control licences or permit stalking.

Table 2.2: Calculated values for different components of the total deer cost. Venison income and fencing costs are calculated as a mean across years, and the standard deviations are given in brackets.

Component	Mean/value (± standard deviation)
Venison income (V)	66,087.30 (± 19,844.88)
Deer control licence income (DCL)	21,000
Permit stalking income (S)	22,000
Fencing costs (F)	38,265.59 (± 25,938.15)
Ranger costs (R)	238,935

Figure 2.14 shows the overall total deer costs (D) for each management option. Note that the scale is cost, as the overall values of D are negative. Reflecting the total replanting costs, the greatest overall deer cost was for other conifer monoculture, closely followed by broadleaved. The lowest cost was for conifer and broadleaved mixture, followed by conifer mixture and Scots pine monoculture, which had similar values.

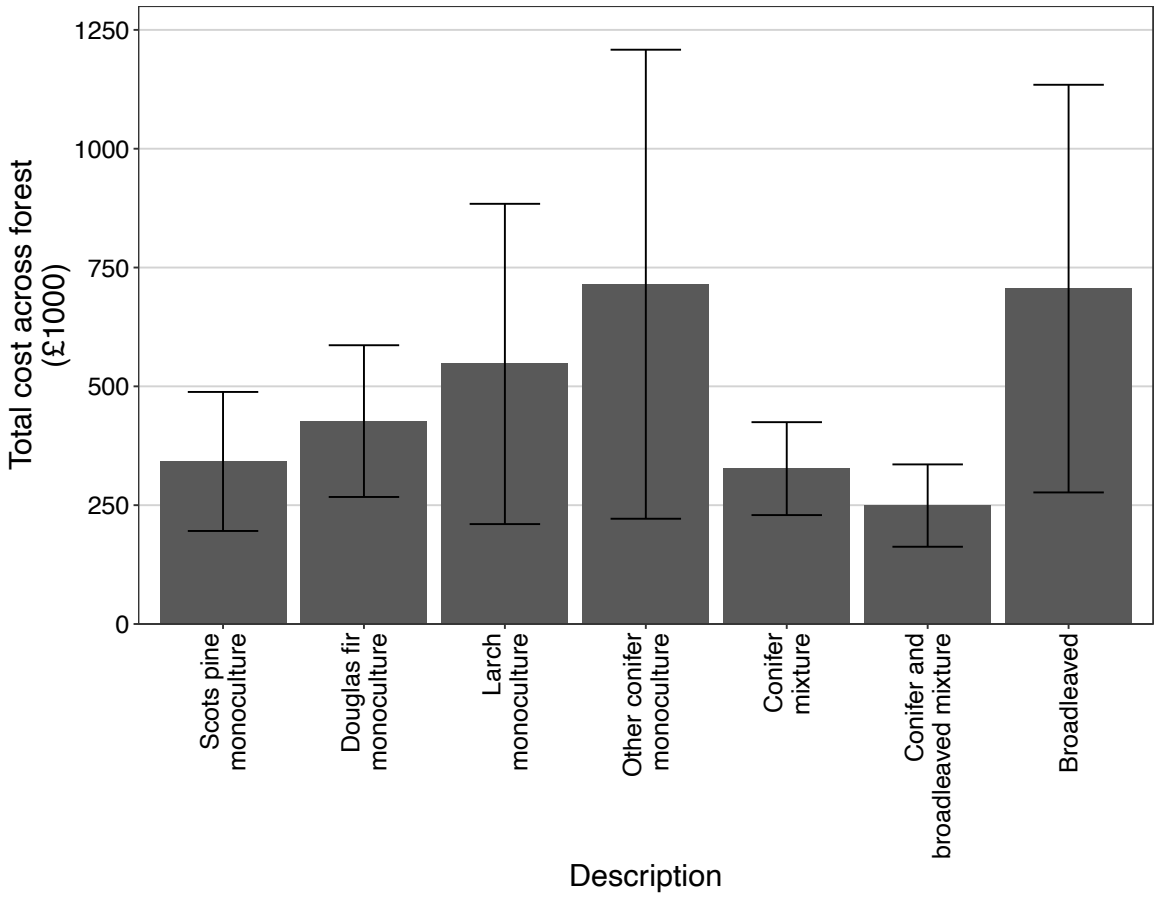

Figure 2.14: Total deer costs for each management option, calculated as a forest-wide value. Bars indicate the mean values, error bars indicate the standard deviation.

Comparison across ecosystem services

There were trade-offs between management options for the three different ecosystem services (Figure 2.15). The best management options for timber production potential were not necessarily the best for carbon and deer. For example, eucalyptus was best for timber, but western hemlock, western red cedar *Thuja plicata* and Douglas fir monocultures and conifer mixtures with a Scots pine pioneer were better than eucalyptus for carbon. The best options for deer were conifer and broadleaved mixtures or conifer mixtures, but they generally delivered medium levels of timber and carbon. When the scaled values across the ecosystem services were added together for each management option, eucalyptus had the highest overall value, closely followed by conifer mixture with a Scots pine pioneer and Douglas fir monoculture. Broadleaved monocultures (except eucalyptus), broadleaved mixtures and Serbian spruce monocultures were the worst options overall, delivering low values of timber and carbon and being highly negative for deer.

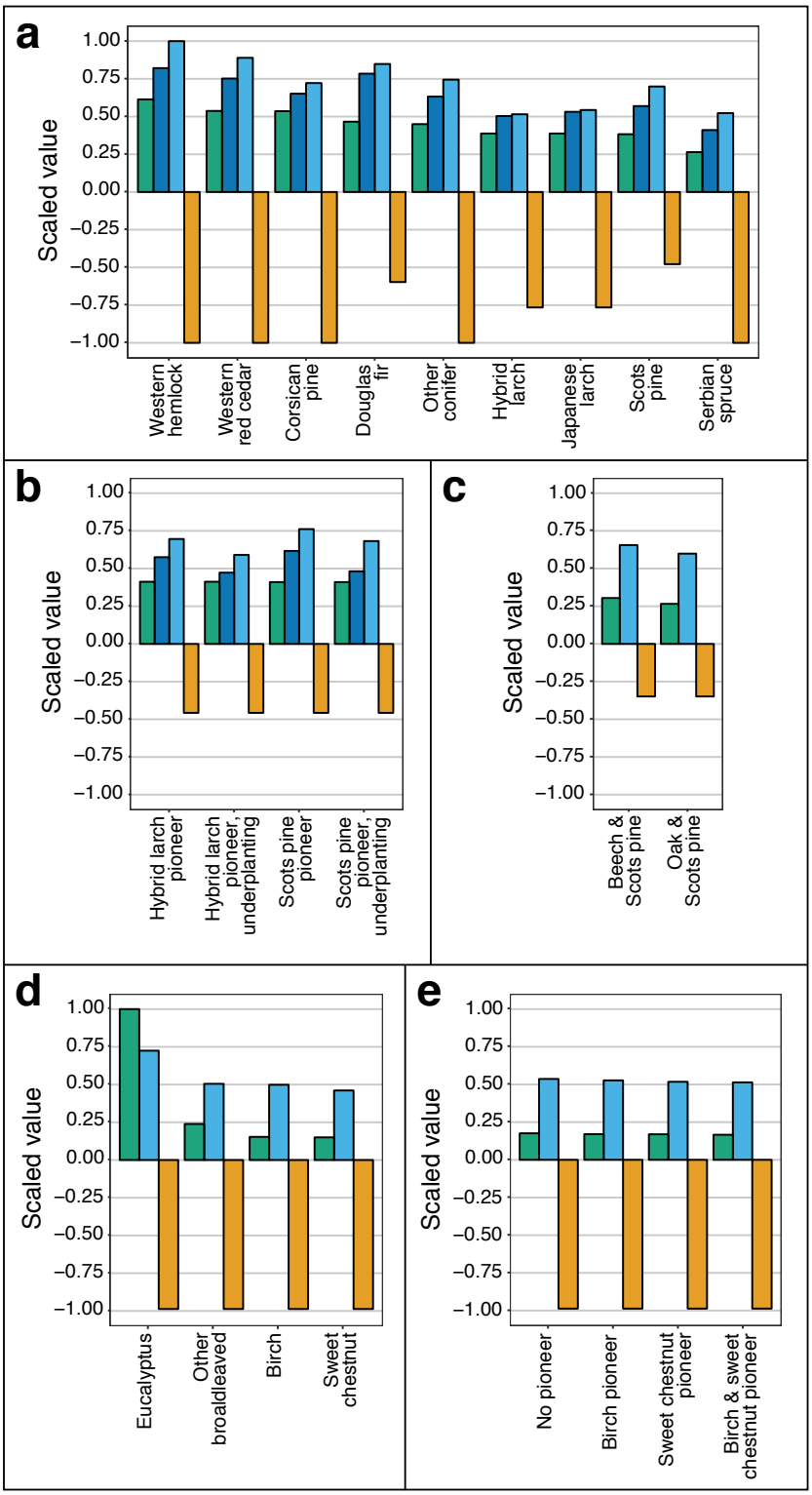

Figure 2.15: The scaled values for timber, carbon and deer for all the management options. Management options are ordered by decreasing timber potential. Colours of bars indicate different services, as follows. Green: timber, dark blue: carbon (managed as clearfell), light blue: carbon (managed as continuous-cover), orange: deer. Conifer and broadleaved mixtures, broadleaved monocultures and broadleaved mixtures were only assessed as continuous-cover. (a) Conifer monocultures. (b) Conifer mixtures. (c) Conifer and broadleaved mixtures. (d) Broadleaved monocultures. (e) Broadleaved mixtures.

DISCUSSION

The relative growth rate and timber production of different tree species is affected by factors such as soil type and climate [95]. Therefore, to assess the timber production potential from management alternatives in a forest, it is necessary to incorporate locally-specific performance expectations of different species. By calculating the average yield classes achieved by each species in Thetford Forest, and interpolating between available yield class curves to adjust values to the same planting spacing, my calculations of timber production potential were as comparable and representative of the study site as possible, given available data.

The results for timber production potential demonstrate the general dominance of conifers over broadleaves in terms of timber and illustrate why the forestry industry has historically focused on even-aged conifer monocultures when timber was the main objective (Figure 2.7) [70]. In particular, western hemlock, western red cedar and Corsican pine monocultures scored highly, as they achieve high average yield classes in Thetford Forest. Interestingly, the results for different conifer species in mixture were fairly uniform, reflecting a decrease in the yield class of western hemlock and western red cedar when in mixture. A hybrid larch pioneer was better than Scots pine, although the differences were only very slight. Given the potential mortality problems associated with the infection of larch by *Phytophthora ramorum*, Scots pine may prove to be a more suitable option for conifer mixtures [96]. Eucalyptus was by far the highest scoring management option for timber. Despite this, it is unlikely to become a dominant component of the Thetford Forest landscape due to its high water-use requirements (the region has low annual precipitation) [97]. Other than eucalyptus, broadleaves had low timber production potential, and even conifer and broadleaved mixtures did not outperform any conifer option except Serbian spruce.

Clearly, not all species are compatible together in mixtures and so it is essential to choose species that are not only suitable to the site, but also complementary in their functional and structural traits [53,98,99]. In this study I used species combinations that are likely to be successful in Thetford Forest and are possible options for future management, selected through consultation with the planning foresters. Various studies have shown that species mixtures can lead to greater forest productivity than monocultures, although evidence is mixed and the mechanisms are poorly understood [53,78,100–102]. I did not incorporate such factors in my analysis and it is therefore possible that the calculated timber production potential values of mixtures are conservative. Furthermore, the relative abundance of species in mixtures is likely to be important, although I assumed equal proportions between species [103,104]. The analysis was an evaluation purely of timber production potential and so did not include the relative commercial values or product uses of different species, which of course can be variable [76]. However, desired timber attributes will change over time in response to market pressures and policy objectives (such as increased demand for woodfuel) [70]; by analysing just the

timber production potential the analysis has retained the flexibility to incorporate these considerations subsequently.

Carbon stocks vary greatly over the lifecycle of a forest stand, with rapid carbon accumulation during the full vigour phase of growth followed by slowing accumulation as the stand reaches maturity, and finally carbon loss after harvesting [70,94]. In addition to the carbon stocks of living biomass, evaluations of a forest carbon balance should also include the carbon emissions of the planting and management operations and importantly, the final use of timber products [81]. The type of wood products that are generated, and their subsequent lifecycles, has a crucial impact on the overall carbon balance of the stand [75,80]. In my analysis, I calculated an indicator of total carbon storage over time, rather than an annual sequestration rate. In Thetford Forest, there is practically no transferral of carbon to long-term soil carbon pools (see chapter 3), and therefore differences in the long-term sequestration rates between management alternatives are negligible. However, there can be much greater differences in the average carbon storage between management options as some systems accumulate and store carbon for longer periods.

Due to an absence of data calibrated for continuous-cover systems, I assumed that carbon accumulation in living biomass was equivalent under both clearfell and continuous-cover systems. This is a simplification as growth regimes will certainly differ between the management types. However, my modelling approach – whereby a different proportion of the stand is harvested at regular intervals – more closely represents techniques such as strip or small group felling, which may be a more realistic alternative to true uneven-aged management, offering a compromise between operational and economic efficiency and increased forest resilience. I also did not account for substitution effects, which is the avoided consumption of fossil fuels (either directly or in the manufacture of other products) in favour of wood-based products generated from forestry [75,81]. Clearly, the scale of substitution effects is dependent on many factors, such as what products are generated from forestry, whether they result in a shift in resource use and the associated emissions from transport of the products. Nevertheless, substitution effects often contribute significantly to calculated carbon balances and so my calculations are likely to be an underestimate [75,81]. Notably, my assessment of the carbon balance in this chapter does not include the soil stocks or dead organic matter. Other studies have found mixed or no effects of management regime on soil stocks; I explore this in detail in chapter 3 [75,105,106].

Similarly to the timber results, western hemlock was the best conifer monoculture option for carbon while Japanese larch, hybrid larch and Serbian spruce were the worst conifer monoculture options (Figure 2.8). However, whereas there was a clear divide between conifers and broadleaves for timber, this was not the case for carbon, as the broadleaves had carbon indicator values that were comparable to several of the conifer options. Broadleaves typically have a higher wood density and non-timber fraction than conifers so store more carbon, although the higher yield classes achieved

by conifers in Thetford Forest largely compensated for this [94]. The exception, of course, was eucalyptus, which had a relatively high yield class and therefore higher carbon indicator value than many conifers (although the exact value is uncertain as a carbon model has not been developed for eucalyptus, so oak values were used instead, as specified in the accompanying guidance; Table 2.1).

I found that continuous-cover consistently outperformed clearfell management alternatives for carbon, complementing similar results found in the small number of studies that make this comparison [79–81]. I used rotation lengths for clearfell options according to current practice of achieving optimal harvesting sizes, but rotation lengths are highly likely to change in future; while there are widespread trends of shortening rotations in response to increasing wood supply or avoiding loss from climate or disease damage, there are also a variety of policies aimed at increasing rotation length for conservation objectives [107–109]. Clearly, increasing the rotation length of clearfell stands increases the carbon stock in biomass and therefore reduces the difference between continuous-cover or clearfell management (Figure 2.9) [107,110]. When projections into the future were over shorter periods (100 or 200 years), increasing the rotation length of clearfell options could even outperform the continuous-cover alternative. However, the relative value of continuous-cover compared to clearfell increased when measured over longer time periods, in addition to changes in the ranks of different species compositions (Figure 2.11 and Figure 2.12). This was the particularly the case when increasing the time period over the short-term (e.g. from 100 to 200 years) as opposed to the long-term (e.g. from 500 to 1000 years). Evidently, the time horizon of interest alters the management recommendations for carbon (as found in other studies, e.g. Pukkala [2017] [111]) and determines the relative value of changing rotation lengths as opposed to switching from clearfell to continuous-cover management alternatives. It is therefore important to give careful consideration to the most appropriate time period over which to project measurements. Forestry operates over long time-scales but obviously there are many factors that may change land use in future; a time period of 200 years is a sensible compromise that includes the effects of multiple stand rotations without projecting too far into the future. Over this time period, I found continuous-cover to be convincingly better than clearfell strategies.

Growth models that reflect the irregular structure of continuous-cover stands are now being developed and calibrated for timber species in the UK, but these are still at early stages and thus I was unable to compare clearfell to continuous-cover management strategies for timber [55]. However, yield is likely to decrease and various studies suggest that production from continuous-cover management is around 80% of that produced from clearfell systems [70,75,76,112]. Furthermore, there are a variety of practical challenges in converting forest stands to continuous-cover, notably intense browsing pressure from deer preventing natural regeneration (although Thetford Forest is free from some of the challenges that are found in the uplands, such as wind risk and the operational difficulties of wet soils) [55,113]. Nevertheless, increasing forest complexity is seen as an important

approach for increasing forest resilience to climate change and disease pressures, and management approaches such as underplanting (whereby faster growing species are used as nurse crops for shade-tolerant, slow growing species) can increase timber production, diversity and value [53]. My modelling suggests that clearfell strategies have a carbon value that is around 80-90% of continuous-cover alternatives. Therefore, the trade-off between timber and carbon of the different management techniques appears to be roughly comparable in the Thetford Forest landscape, suggesting that a mix of both strategies would be appropriate.

Clearly, deer pressure has a substantial impact on the forest, and the success of clearfell or continuous-cover strategies depends to a large extent on successful deer management. When natural regeneration is successful, continuous-cover management can be as or more profitable than clearfell strategies [114]. There was high variation in the percentage crop damage caused by browsing pressures (Figure 2.13a) and it was not possible to assess some options individually due to lack of data (e.g. western hemlock). Nevertheless, the results indicate that Scots pine monoculture and conifer and broadleaved mixture may be more suitable options for continuous-cover management than broadleaves and other conifer monoculture, due to lower average browsing damage. However, all options had relatively high damage (means were between 24.8% and 44.8%), suggesting that relying on natural regeneration without mitigating for deer impacts is unlikely to be a feasible management strategy.

A similar trend followed through to calculations of overall deer costs: conifer and broadleaved mixture had the lowest total cost, whereas other conifer monoculture and broadleaved options had the highest costs (Figure 2.14). There was substantial variation, both between options (the highest mean total costs were almost three times as high as the lowest) and within different options, reflecting the variability in source data and making it difficult to draw clear conclusions about the difference between management options. Nevertheless, the results illustrate the extent of the overall costs of high deer populations on forest management, which cannot be compensated for by the income generated through venison production or recreational hunting. Based on present deer density levels, it is difficult to envisage how this cost-benefit balance could be shifted. Deer management across the forest is an essential activity to maintain deer populations at their current level and prevent further increases (high densities at the wider landscape scale make it very difficult to reduce overall numbers due to source-sink dynamics [83]). An alternative option would be to switch the investment of resources from population management into protection measures such as fencing, but this is a short-term solution that is likely to be more costly than population management in the long-term. Other strategies such as planting sacrificial crops, which are more attractive to deer, may reduce pressure on timber crops, although this would involve costs in terms of the plants, operations and land not being used for forestry. Without detailed experimentation, it is difficult to predict whether this could be cost-effective. At present, deer management costs cannot be easily reduced

without accepting much greater crop damage, potentially rendering commercial forestry unviable. Income from venison, deer control licences and stalking permits are a by-product rather than an objective of deer management. These income revenues cannot be increased without reducing the culling efficiency of the wildlife ranger teams and therefore increasing crop damage. My analysis did not take into account the benefits of deer as a cultural ecosystem service. Deer are undeniably a key wildlife attraction for visitors to the forest, although they are not commonly seen by visitors, being shy animals with a large forest resource (only 2.5% is within 10 m from a main path or track). Given this, and their extremely high landscape population sizes, it is currently inconceivable that deer densities could be reduced through management to a level where the cultural ecosystem service is compromised, and therefore this does not influence the investment into population management and associated costs. Furthermore, as they are fairly wide-ranging and elusive, it is unlikely that different types of management options deliver significantly different levels of cultural benefit from deer sightings. To determine whether the overall cultural value of deer negates their management costs, further research could use techniques such as willingness-to-pay to elucidate how greatly they are valued as a cultural ecosystem service [115].

Bringing together the values of timber, carbon and deer for each management option, it is clear that broadleaves are the worst options, with very low values across all three ecosystem services (Figure 2.15). The exception is eucalyptus, which has high timber and carbon values. However, as a non-native species with high water requirements, it is unlikely to become a major component of the Thetford Forest landscape. Whereas the differences between timber and carbon values are fairly gradual, there are stark contrasts between the calculated values for deer. This is likely to be at least partly due to the fact that deer values could only be calculated for a limited number of management options due to data availability, as many of the conifer options are relatively novel species in Thetford Forest. As a result, options such as Douglas fir or conifer mixture with a Scots pine pioneer were valued highly overall when the three ecosystem services were combined, as they had much lower deer costs for relatively small compromises from maximum timber and carbon values. However, it is important to bear in mind that the calculations for deer also involved the greatest uncertainty due to high variation.

Overall, a combination of clearfell and continuous-cover management is likely to deliver high timber and carbon values, while also delivering greater forest resilience and diversity. Deer pressures are a major ecosystem disservice and challenge to forest management, particularly if continuous-cover systems need to rely on natural regeneration. Current results suggest that Scots pine monoculture may be a successful continuous-cover option, suffering relatively low deer damage and delivering moderate carbon value; it is also regenerates easily on poor, sandy soils such as those at Thetford Forest [116]. Other options to explore for continuous-cover management include Douglas fir, which delivers high carbon value but appears to suffer less deer damage than other

conifers (although may not regenerate as easily), or conifer and broadleaved mixtures, which have low deer damage and outperform various conifer species in terms of carbon. Further trials are needed to explore whether such options are viable under current deer browsing pressures. In terms of clearfell management strategies, western hemlock and western red cedar would maximise timber values, although there is currently insufficient data to evaluate deer impacts for these species individually. Corsican pine is no longer planted in the forest due to infection from *Dothistroma septosporum*. However, conifer mixtures and Douglas fir monoculture may be good choices for clearfell management, with relatively low deer damage and high timber delivery. In conclusion, a diversity of conifer options is likely to deliver the greatest timber and carbon benefits, alongside increased forest resilience, while minimising the costs arising from deer damage.

3 | Afforestation on sandy heathland has little effect on soil quality or carbon and nitrogen storage

SUMMARY

Thetford Forest was planted almost 100 years ago and therefore we might expect that afforestation will have had led to substantial changes in soil properties during this time. However, the underlying soils are generally low quality and sandy, with low capacity for the accumulation of organic matter. Therefore, in this chapter I explore if and how the establishment and management of Thetford Forest has mediated soil changes by comparing forest sites to historic heathland in this landscape. I conducted an extensive soil sampling survey, analysing soil layers for indicators of soil quality (total carbon, total nitrogen, carbon to nitrogen ratio) and calculating carbon and nitrogen stocks. Soil quality indicators gave mixed outcomes for the best management options, but overall the difference between management options was marginal. For carbon stocks, the fermentation layer was of crucial importance, especially under conifers where a thick layer accumulates, as there is relatively little carbon transfer to the sandy mineral soil. Similarly, nitrogen stays in organic material rather than being incorporated into the mineral layers. This emphasises the importance of promoting forestry management that disturbs the soils as little as possible so such accumulated carbon and nitrogen in the organic layers is not lost through leaching or respiration. The underlying physical properties of the soil in the Thetford Forest landscape limit the scope of land use to deliver soil quality improvements or carbon storage. This conclusion is particularly important given repeated pledges by governments to tackle climate change through afforestation, emphasising that consideration of factors such as soil type is essential.

INTRODUCTION

Soils are the fundamental resource of forestry [66,117]. They are crucial to the growth and performance of forest trees as they provide nutrients and anchorage, store and filter water, and determine the choice and growing potential of tree species [118–120]. Different tree species have adapted to different soil types and climates, and many tree species significantly modify soils [95,121,122]. The UK forestry industry has great experience in selecting timber species that are suitable to different sites.

However, to establish further rotations of trees successfully it is crucial to understand, not only how soil type affects tree growth performance, but also how previous rotations have affected soil conditions. In light of climate change and disease concerns, forest management across the UK is rapidly changing from the rotational clearfelling of monocultures to more resilient mixed species, multi-age stands and more complex silvicultural systems, such as continuous-cover forestry [123,124]. Furthermore, the role of woodlands and forests as a carbon sink and for greenhouse gas mitigation is becoming increasingly important, so wide-scale woodland planting has been pledged by many UK governments [71,72,125,126]. Soils are the least renewable component of the forest ecosystem, and future sustainable forest management must take soil conservation more fully into account [51,117]. It will be imperative for forest managers to understand the temporal relationship between soils, tree species choice and management practice.

In addition to timber production and carbon sequestration, forests provide a variety of important ecosystem services, such as water purification, flood defence and recreational amenity [12,46,127,128]. Soil formation is an important supporting service, underpinning the delivery of many of these final ecosystem services [10]. Furthermore, soil quality is itself classified as a regulating ecosystem service, due to its important role in regulating the environment, such as capturing nutrients and carbon, purifying water and buffering against atmospheric pollutants [11]. It is therefore essential to understand how current management practices are influencing the soil, and whether they enhance or compromise the delivery of ecosystem services.

Typical indicators of soil quality in ecosystem services assessments are total carbon concentration, total nitrogen concentration, and the carbon to nitrogen ratio (C:N) [20]. Total carbon concentration and total nitrogen concentration usually correlate with each other and with soil quality. Soil carbon has a major role in influencing other important biological, chemical and physical soil properties and is an indicator of soil organic matter content [129,130]. Soil organic matter is an important source of soil fertility, a nutrient store, provides energy to microorganisms, buffers against pH changes, and increases soil aeration and water holding capacity [11,131]. Nitrogen is an essential nutrient for tree growth. Therefore, the avoidance of leaching and retention of nitrogen is an important soil function [132,133]. A high C:N ratio can be an indicator of poor soil quality: during decomposition of organic matter, nitrogen is largely retained and recycled within the soil whereas carbon is mineralised to carbon dioxide, so a lower C:N ratio indicates more thorough decomposition of organic matter [134]. A low C:N ratio may relate to better soil quality as there is more nitrogen available for vegetation uptake; in contrast, a high C:N ratio may be the result of microbial nitrogen immobilisation, leading to lower productivity [135].

Additionally, carbon stocks are a widely-used proxy for climate regulation. It is important to note that as carbon stocks are a static measure, they do not strictly measure the ecosystem service of climate regulation (e.g. the carbon sequestration process or carbon storage over time) [20]. However,

they provide an important baseline for future monitoring, and can be informative in the comparison between different habitat types or management strategies [136]. In forests, the soil carbon stock is particularly important as it normally contains an equivalent or even greater proportion of the carbon stock than above-ground biomass [129,136–138].

In this chapter, I will calculate the carbon and nitrogen stock of the soils under Thetford Forest and explore these three indicators of soil quality. Studies of UK forests show mixed results in whether soil organic matter or total carbon accumulates over time [118,139,140]. Nevertheless, given that the majority of the Thetford Forest site was afforested almost 100 years ago, it is reasonable to predict that there have been significant changes to the soil since forest establishment, which we can measure now as the difference between the forest and historic heathland sites. However, soils across the landscape are generally sandy [57], with low capacity for the accumulation of organic matter and thus limited potential for changes to soil quality mediated through vegetation changes. Therefore, this study sets out to elucidate the extent to which such changes, if any, have occurred, and how this has been influenced by forest management practices (such as species choice). For each ecosystem service, I quantify the differences between different management options and land use, the effects of historical soil type (acidic or calcareous), and the difference between soil sample layers.

METHODS

Plot selection

I selected forest plots to represent a variety of different land use and management options across the forest based on a GIS analysis. I used the soil map from the 1973 Breckland Soil Survey to ensure that both calcareous and acidic plots were identified for soil sampling for each management option (Table 3.1). Plots were only selected if the main tree or vegetation component was planted more than 15 years ago, to ensure that the crop was well established. Plots were selected that exceeded 2 ha (with the exception of one plot that was found to be sub-divided by species and therefore each section was smaller). The conifer monocultures comprised of Corsican pine, Scots pine, hybrid larch, Douglas fir or Weymouth pine *Pinus strobus*. Species in broadleaved monocultures were sweet chestnut, eucalyptus, oak, beech and birch. Full information on the plots is given in Appendix table B.1.

Table 3.1: Summary of survey plots.

Management option	Category description	Calcareous plots	Acidic plots	Total number of plots
Conifer monoculture	One species, conifer	2	4	6
Conifer mixture	3+ species, all conifer	3	3	6
Broadleaved monoculture	One species, broadleaved	2	3	5
Broadleaved mixture	3+ species, all broadleaved	3	2	5
Mixture (primary conifer)	3+ species, combination of broadleaved and conifers, largest component is conifer	2	3	5
Mixture (primary broadleaved)	3+ species, combination of broadleaved and conifers, largest component is broadleaved	3	2	5
Open (cleared)	Sites recently cleared from forestry to revert to heathland (~15 years ago)	3	2	5
Heathland	Historical heathland sites, never planted	3	2	5
Total				42

Sampling procedure

Soil sampling took place in November and December 2016. At each plot, I selected three sub-plots by randomly generated coordinates. I collected samples from the organic and mineral layers (Figure 3.1a). In forested sites, the organic layers were separated into the leaf litter layer (intact leaves or needles) and the fermentation (F) layer (partially broken-down leaf material and humus). In open sites, the organic layers also included a grass layer, but leaf litter was sometimes not present. The mineral layers were separated into three different depths below the F layer: 0-5 cm, 5-10 cm, 10-20 cm.

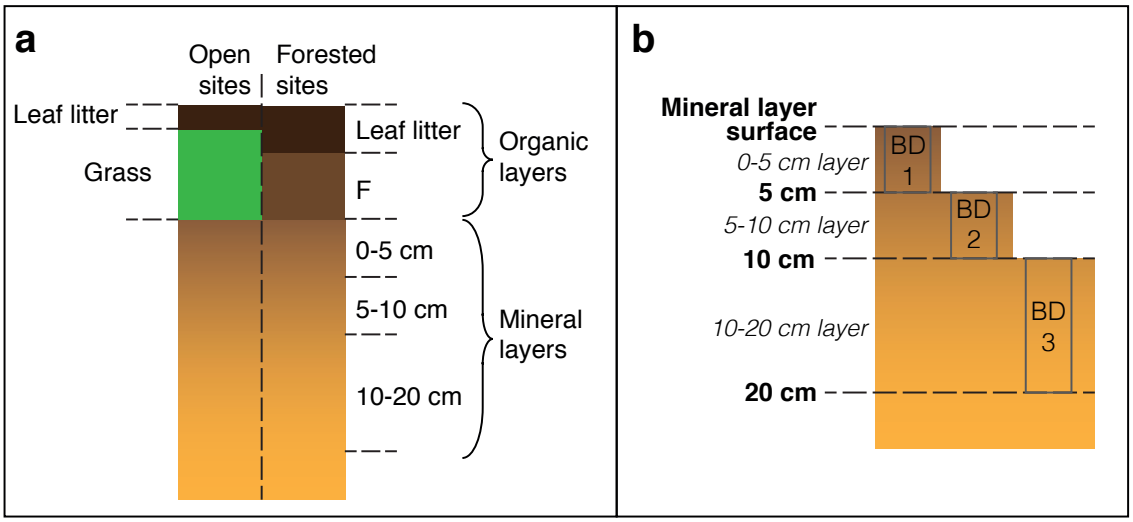

Figure 3.1: Diagram of soil samples. a) All soil layers sampled. The leaf litter and F layers may vary in depth. b) Samples taken to calculate bulk density of different layers. BD1, BD2 and BD3 indicate different bulk density samples, in increasing order of depth.

At each sub-plot, I tapped down a 2-inch diameter soil corer until the top of the core was level with the top of the leaf litter (the full length of the soil corer including the nose was 35.5 cm). While still in the ground, I unscrewed the top of the corer and measured the compression of the sample by placing a marked metal tube in the top of the corer. I then dug up the corer and carefully lifted it from the ground so that soil was not lost from the bottom of the corer. I collected mineral layers from the corer for all sites, and also the organic layers from the corer in open sites. In forested sites, I collected all organic layer material within a 25 x 25 cm quadrat adjacent to the corer.

In addition, at the first sub-plot, I took extra samples to calculate mineral soil bulk density, which was used in subsequent calculations of total carbon or nitrogen stocks. I cleared the surface litter and F-layer from the soil and tapped the corer down to 5 cm (0-5 cm sample – BD1 in Figure 3.1b). I then excavated an adjacent area of soil to 5 cm depth and tapped the corer down another 5 cm (5-10 cm sample – BD2 in Figure 3.1b). Finally, I excavated an area of soil to 10 cm depth and tapped the corer down another 10 cm (10-20 cm sample – BD3 in Figure 3.1b). This ensured that each bulk density sample was minimally affected by compression as the corer was tapped down; if all samples were taken from one core, the top of the sample would undergo more compression than the bottom, affecting bulk density calculations.

I recorded the time, date and GPS location of each sub-plot. I transferred samples to a fridge as soon as possible on the sampling day and stored them at 4°C until analysis.

Laboratory analysis

Samples were transferred to the Forest Research chemical laboratory at Alice Holt. The bulk density samples were weighed, dried at 105°C, and then re-weighed. I calculated dry bulk density of the mineral soil layers by dividing the dry weight by the volume of the sample (calculated as the corer was two-inch diameter). Moisture content of the organic layer samples were determined from the weights of wet and oven-dried (at 40°C) samples. I calculated the litter, F and grass layer densities by dividing the dry weight by the volume of the sample (25 x 25 cm quadrat multiplied by measured thickness of the layer).

Soil samples for chemical analysis were also oven-dried at 40°C until dry (assessed using visual inspection). Litter, F-layer and soil samples were then individually sieved (2-mm) and milled. The samples were then analysed for total carbon (separated into organic carbon and inorganic carbon) and total nitrogen by dry combustion at 900°C, with a C/N analyser. These values were then corrected for the residual soil moisture content in each sample. Soil pH (in water) was also measured in each sample.

Data analysis

The C:N ratio was calculated as the total organic carbon concentration divided by the total nitrogen concentration. For each soil layer, I calculated the mean value of each variable per plot from the values at each of the three sub-plots. For some litter, F and grass samples there was insufficient material to accurately assess pH, so means were taken of the available data. For each plot and soil layer, I calculated carbon stocks by multiplying the mean moisture corrected total carbon concentration (organic and inorganic carbon), the mean thickness of the layer, and the mean density (bulk density for mineral soil layers, and density for litter, F and grass layers). I calculated total plot carbon stock by summing the carbon stocks of each sample layer. I followed the same method to calculate nitrogen stocks.

From henceforth, total carbon concentration refers to moisture corrected total organic carbon concentration (%). Layer carbon stock refers to the total carbon stock in each soil layer, and total plot carbon stock refers to the sum of carbon stocks from all samples per plot. The equivalent terms are used for nitrogen.

For total carbon concentration, total nitrogen concentration, the carbon to nitrogen (C:N) ratio, the thickness of the F and litter layers, layer carbon stock, total plot carbon stock, layer nitrogen stock and total plot nitrogen stock, I fitted a linear model and then used an ANOVA to test for significance. Within these main categories, I also fitted separate linear models to compare different subsets of data; for example, only mineral soil samples. Management option, soil layer, historical soil type (the broad soil type – either acidic or calcareous – as classified by Corbett in the Breckland

Soil Survey [57]) and pH were included as predictors. The full combination of tests is given in Appendix table B.2. I used a Type II ANOVA on the models to determine which predictors were significant. Where predictors had a significant effect, I then used a Tukey-Kramer post-hoc test to find pairwise interactions that were significant (although pH could not be included as a predictor at this stage as it was a continuous variable). Before running the Tukey-Kramer I excluded all non-significant predictors from the model (at the 0.05 significance level).

To account for the possibility of increased type I errors through multiple testing of the same dataset, I used a Benjamini-Hochberg procedure to reduce the *P* value [141,142]. I collated all *P* values for linear models (53 in total); with a false discovery rate set at 5% the corrected significance *P* value was 0.0175.

All data were analysed using R[143].

RESULTS

Total carbon and nitrogen concentrations

Soil layer significantly affected both total carbon and total nitrogen concentrations ($P < 0.0001$ for both; Table 3.2). The litter and F layers had the highest average total carbon and total nitrogen concentrations (litter layer greatest for total carbon concentration, F layer greatest for total nitrogen concentration), followed by the grass layer, and then the mineral soil samples in order of depth (Figure 3.2). When a model was fitted just to organic soil samples (i.e. litter, grass and F layers), management option had a significant effect on total carbon concentration ($P = 0.0022$; Table 3.2). Between management options the total carbon concentration in the organic samples of heathland sites were significantly lower than all the forested sites, and total carbon concentration in the organic samples of sites that were recently cleared was significantly lower than conifer monoculture and conifer mixture (Figure 3.2). There was a similar pattern with total nitrogen concentration, although management option was not significant at the Benjamini-Hochberg corrected level of significance.

The litter and F layers had consistantly significantly higher total carbon and total nitrogen concentrations than mineral soil layers. The 0-5 cm mineral layer had significantly higher total carbon concentration than the 10-20 cm layer and significantly higher total nitrogen concentration than both the 5-10 cm and 10-20 cm layers (Figure 3.2).

Across all samples, the mean proportion of total carbon concentration that was inorganic was 2.31%. No inorganic carbon at all was recorded in 504 of the 600 total samples.

C:N ratio

Soil layer significantly affected the C:N ratio (Table 3.2). Similarly to total carbon and total nitrogen concentrations, the litter layer had the greatest C:N ratio, followed by the F layer, grass layer and then mineral soil samples in order of increasing depth (Figure 3.3). Management option had a significant effect on the C:N ratio when models were fitted to organic ($P = 0.0159$) and mineral soil layers separately, ($P = 0.0037$). Management options that had a conifer component (i.e. pure conifer stands or mixtures with broadleaves and conifers) had a significantly higher C:N ratio in mineral layers than heathland sites (Figure 3.3). However, a Tukey-Kramer test did not find any significant pairwise interactions between management options for only organic layers. Additionally, increasing pH was significantly correlated with decreasing C:N ratio for models including all layers or only mineral layers.

Table 3.2: P values for the significance of predictors in all linear models. Dark green shading indicates significance at the Benjamini-Hochberg corrected significance level (0.0175); light green shading indicates significance at the traditional P = 0.05 significance level.

Response variable	Data subset	Predictor variable			
		Management option	Soil layer	Historical soil type	pH
Total carbon concentration	All soil layers	0.5945	<0.0001	0.0525	0.0168
	Only organic soil layers	0.0022	NA*	0.0803	0.5538
	Only mineral soil layers	0.1445	<0.0001	0.4492	0.2455
Total nitrogen concentration	All soil layers	0.1465	<0.0001	0.0269	0.0675
	Only organic soil layers	0.0305	NA*	0.0175	<0.0001
	Only mineral soil layers	0.0839	<0.0001	0.6077	0.9390
C:N ratio	All soil layers	0.3360	<0.0001	0.5977	0.0006
	Only organic soil layers	0.0159	NA*	0.9533	0.0557
	Only mineral soil layers	0.0037	0.0147	0.4199	<0.0001
Layer thickness	Only litter and F layers; all plots with corresponding data	0.5052	0.0026	0.8712	<0.0001
Layer carbon stock	All soil layers	0.0750	<0.0001	0.6084	0.0898
Layer nitrogen stock	All soil layers	0.0111	<0.0001	0.5982	0.6667
Total plot carbon stock	All soil layers	0.0427	NA	0.3175	NA+
	Only mineral soil layers	0.4471	NA	0.7166	NA+
Total plot nitrogen stock	All soil layers	0.2312	NA	0.4910	NA+
	Only mineral soil layers	0.1672	NA	0.8654	NA+

* Not possible to test for influence of soil layer as plot management option determines which samples were collected (i.e. only grass in open sites)

+ pH varies across soil layers so not included

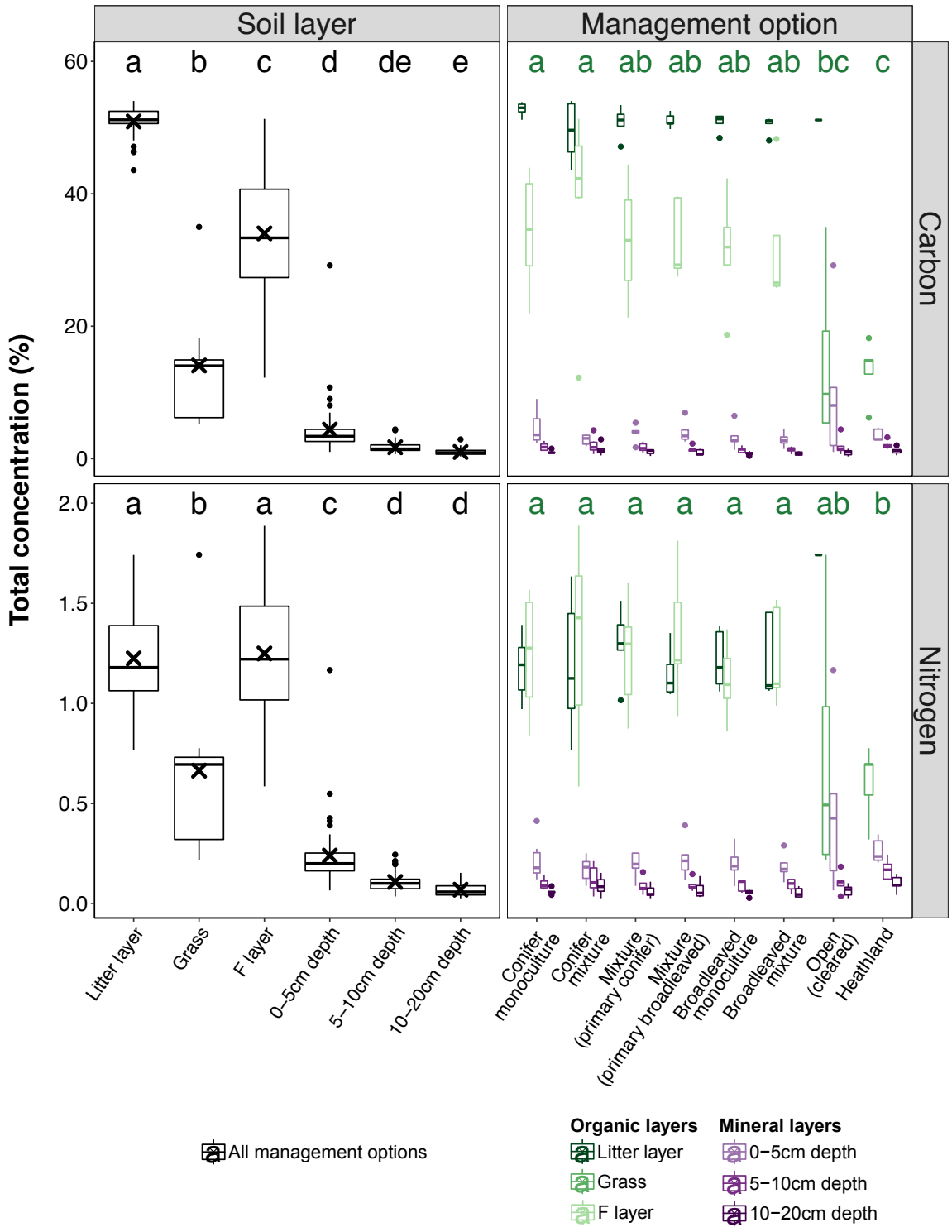

Figure 3.2: Total carbon and nitrogen concentrations of the different soil layers. Left panels show all data across management options, right panels show data separated by management option. Letters show significant differences between groups (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different at P = 0.05. On right panels, letters indicate differences between organic soil samples only. Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers.

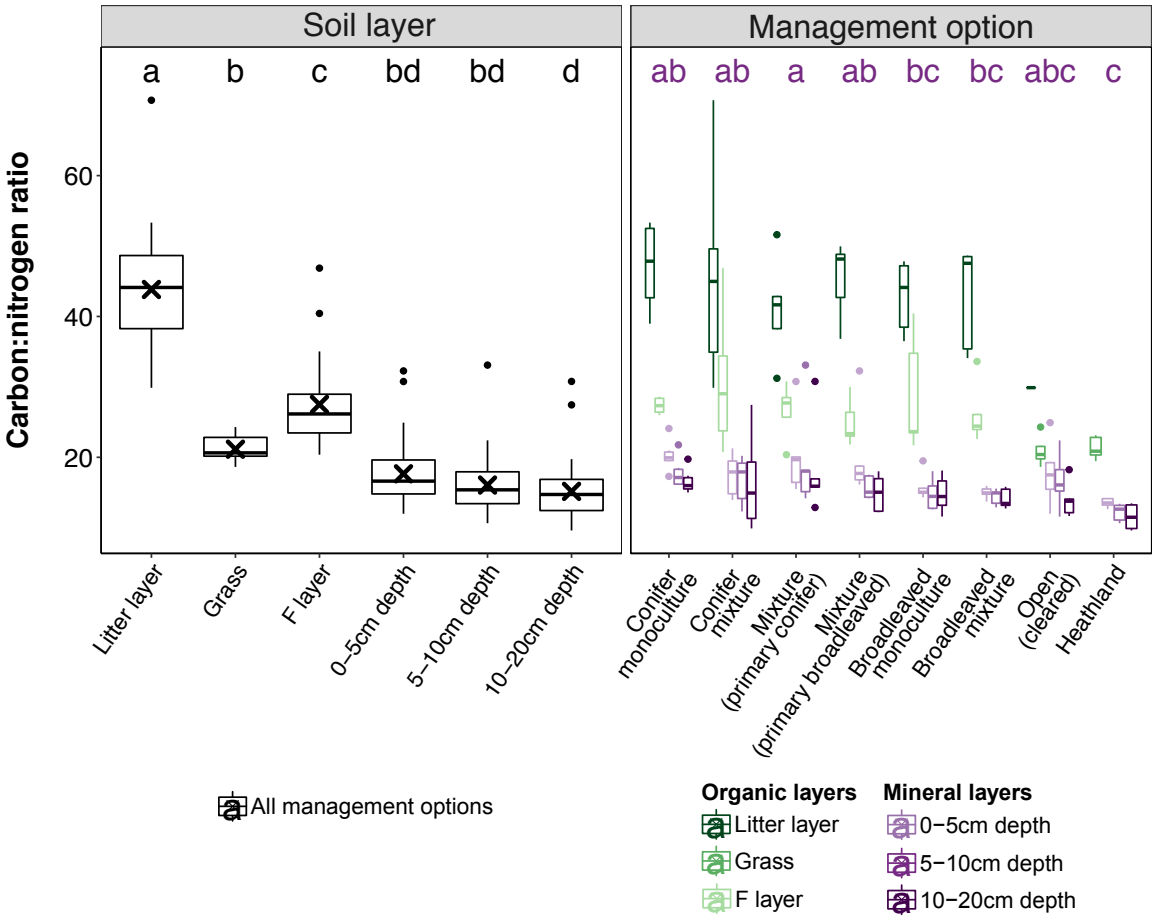

Figure 3.3: The C:N ratio of the different soil layers. The left panel shows all data across management options, the right panel shows data separated by management option. Letters indicate significant differences between management groups (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different at P = 0.05. Letters on the right panel correspond to differences between mineral soil samples only. Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers.

Depth of layers

Neither management option nor historical soil type had a significant effect on the thickness of the litter and F layers, but the soil layer (whether it was litter or F) did (P = 0.0026; Table 3.2). The overall average litter layer depth was 2.0 cm (range of 0.5-4.5 cm), whereas the F layer was generally deeper (overall average was 4.3 cm, range of 0.5-12.0 cm). Broadleaved mixture had the greatest average litter layer depth (2.4 cm), whereas conifer monoculture had the smallest average litter layer depth (1.5 cm) (excluding the open (cleared) site where there was scattered leaf litter) (Figure 3.4). In contrast, the opposite was true for F layer depth, with conifer monoculture having the greatest average thickness (5.6 cm) and broadleaved mixture having the smallest average thickness (2.3 cm) (Figure 3.4).

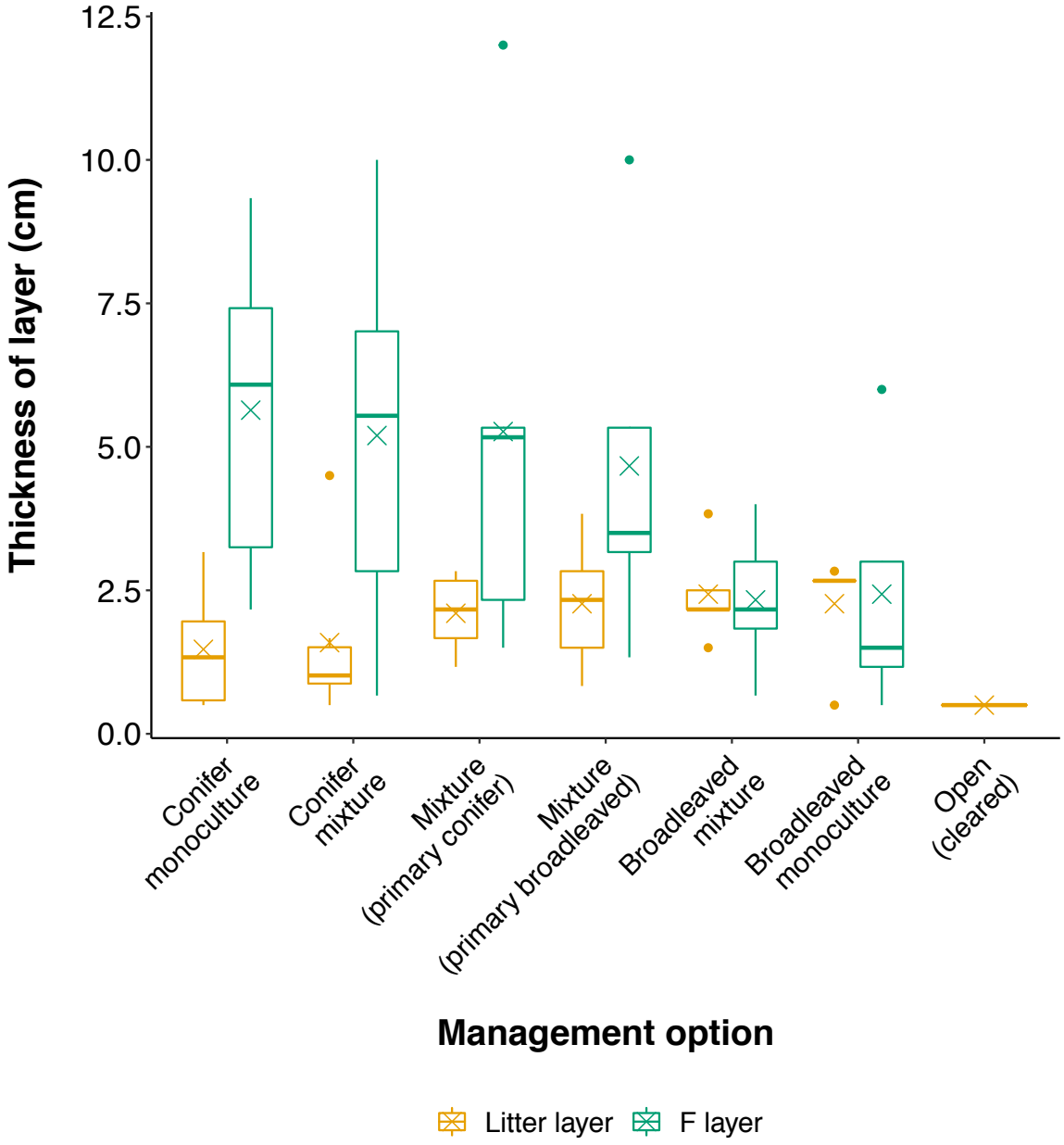

Figure 3.4: Thickness of litter and F layers of different management options. Colours correspond to the layer. Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers.

Carbon and nitrogen stocks

For all plot types with a conifer component (i.e. pure conifer stands and mixtures), the F layer had the greatest carbon stock; in pure broadleaved stands and open plots the 0-5 cm soil layer had the greatest carbon stock (see Appendix table B.3). Soil layer had a significant effect on layer carbon stocks (Table 3.2), whereas management option did not. When all types of management options were grouped together, a post-hoc Tukey-Kramer showed that overall the F layer had the largest carbon stock, followed by mineral soil layers, with leaf litter and grass having the smallest stocks (although the 5-10 cm mineral soil layer was not significantly different from the leaf litter and grass layers; Figure 3.5). There was no difference between the mineral soil layers.

Nitrogen stocks followed a similar pattern. The F layer had the greatest nitrogen stock in conifer stands and mixtures where the primary component was conifer; the 0-5 cm soil layer had the greatest nitrogen stock in mixtures where the primary component was broadleaved, pure broadleaved stands or open plots. Soil layer and management option had a significant effect on nitrogen stock (Table 3.2). A Tukey-Kramer test showed that there was no difference between the F layer, 0-5 cm and 10-20 cm samples (they all had the highest nitrogen stock), and there was also no difference between the mineral soil layers (Figure 3.5). The litter and grass layers had significantly lower nitrogen stock than other samples (Figure 3.5).

When carbon stock and nitrogen stock was summed for each plot, conifer mixture had the greatest average total carbon stock and total nitrogen stock, followed by mixtures (where the primary component is conifer) and then conifer monocultures (Figure 3.5). Broadleaved monoculture and broadleaved mixture had the lowest total carbon stock and total nitrogen stock. The differences were so pronounced that, on average, conifer mixture had over twice the total carbon stock than broadleaved monoculture, and over 1.5 times the total nitrogen stock. However management option did not have an overall significant effect on total carbon and nitrogen stocks (Table 3.2), perhaps due to extensive variation.

In contrast, when only mineral soil layers were added together, open (cleared) sites had the highest total carbon stock and heathland had the highest total nitrogen stock, and there was overall little difference between management options. This demonstrates the importance of the organic soil layers in the overall total stocks. In particular, the F layer played a crucial role in determining the overall total carbon and nitrogen stocks. It had the second highest total carbon concentration (significantly lower than the litter layer, but higher than any other soil layer) and highest total nitrogen concentration, and was also thicker than the litter layer (Figure 3.2 and Figure 3.4). Indeed, the litter layer was usually so thin that its contribution to total stocks was negligible, whereas for conifer mixture the F layer alone contributed a greater carbon stock than all the mineral layers combined. Generally thicker F layers under conifers led to higher total stocks.

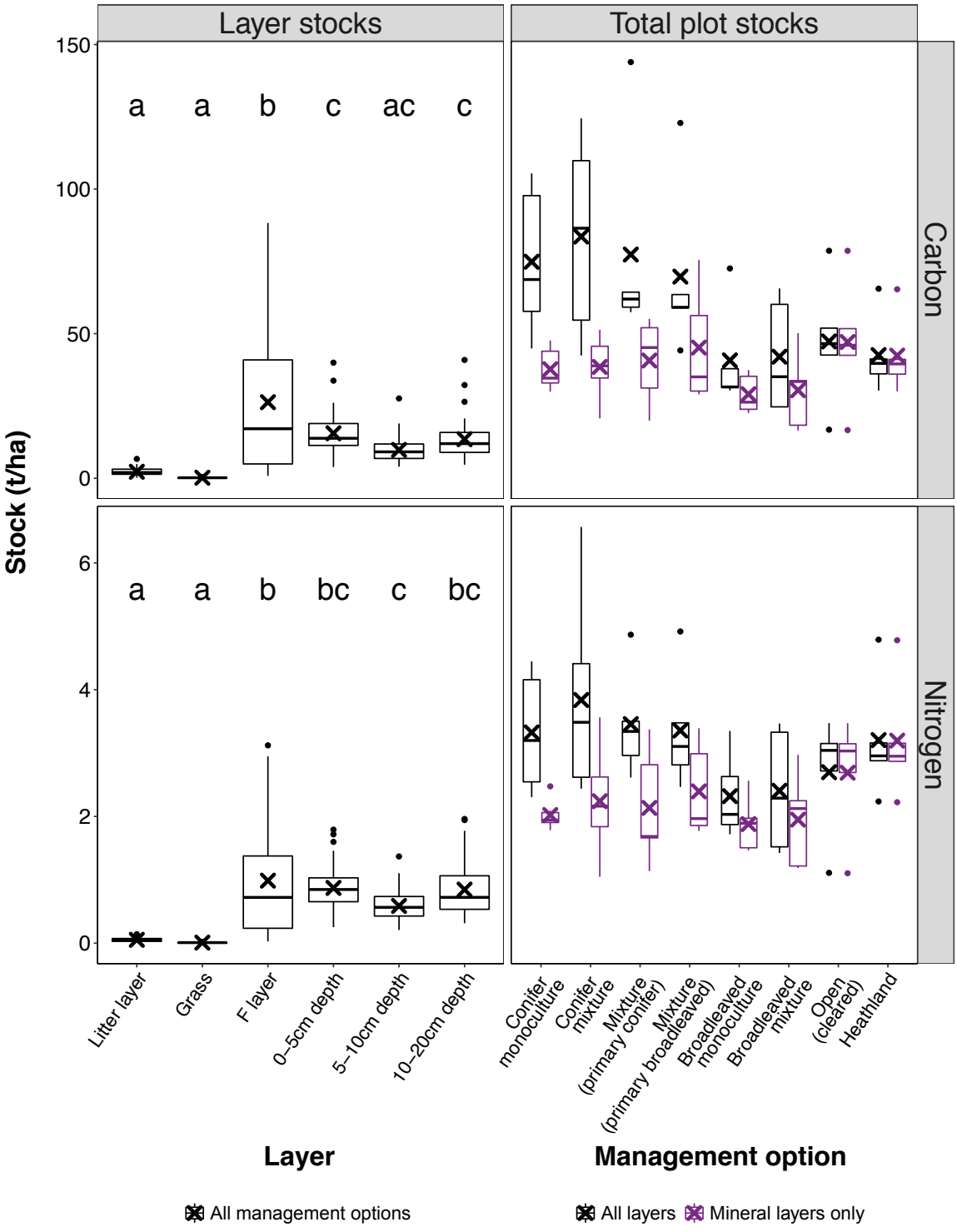

Figure 3.5: Carbon and nitrogen stocks. Left panels show the layer stocks across all management options. Right panels show the total plot stocks for each management option; black values correspond to the total plot stock of all the layers, purple values correspond to the total plot stock of just the mineral layers. Boxplots with different letters indicate significant differences between soil layers (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different, at $P = 0.05$. Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers.

DISCUSSION

Carbon

Afforestation has long been posited as a way of sequestering carbon and tackling climate change [12,144], and the UK government has pledged wide-scale woodland planting[71]. The soil carbon stock is particularly important as it often contains a greater proportion of the carbon stock than above-ground biomass [136,138]. This study has demonstrated the importance of the F layer in determining carbon stock in Thetford Forest. Under conifers, the carbon stock in the F layer was much greater than under broadleaves, as expected given the faster decomposition rates of broadleaved organic matter, but in contrast to findings from national studies (which found higher F layer carbon stocks under broadleaves, probably due to higher average F layer density under broadleaves than conifers) [136,145]. As the majority of the total plot carbon stock is in the F layer, it is very vulnerable to being lost through aeration or leaching if the F layer is disturbed. This has particular relevance to forest management operations, given the importance of long-term carbon sequestration and storage to mitigate climate change. The UK Forestry Standard outlines guidelines to minimise soil disturbance during forestry operations [66] – these results emphasise their importance.

Although soil layer significantly affected total carbon concentration and layer carbon stock (Table 3.2), there was no difference between the different mineral soil layers (with the exception of the 0-5 cm layer having significantly greater total carbon concentration than the 10-20 cm layer) (Figure 3.2 and Figure 3.5). Additionally, total carbon concentration in any of the mineral soil layers was very low compared to the litter and F layers. Although it was not possible to look at changes over time, these results suggest that carbon is only very slowly being transferred into soil pools from the litter and F layers. Many studies of existing UK forests find either no or very small increases in total carbon concentration and carbon stocks over time in upper soil layers [118,139,140,146]. While there is some evidence from northern Europe that afforestation on heathland or cropland sites leads to significant increases in soil organic carbon stocks in the uppermost soil mineral layers [147], this has not been found in this study. Not only has afforestation not yet led to an increase in mineral soil layers carbon stock, but total carbon concentration is also not increasing rapidly in the soil layers. This is not surprising: the soils in Thetford Forest are very sandy (so will not easily bind and accumulate carbon), and the regional rainfall is low (with very low drainage and hence limited leaching) [148], so there is limited opportunity for carbon to be incorporated into the mineral soil profile. Nevertheless, given that soil carbon stock is such an important contributor to overall carbon stock in forest ecosystems [136], and the routine advocation of forestry planting for carbon sequestration and storage purposes, it is noteworthy that after nearly a century of afforestation in Thetford there has been such little transferral of carbon to the mineral soil layers. With the

continuing soil acidification observed (see chapter 4) and the associated changes in microorganism diversity and abundance (particularly earthworms) leading to reduced cycling of organic matter, this lack of carbon incorporation into lower soil layers is only likely to be exacerbated in future.

Nitrogen

Thetford Forest receives some of the highest nitrogen deposition in the United Kingdom (13-19 kg N ha^{-1} yr^{-1}), and various areas of the forest are nitrogen saturated [148–150]. This is well above the European threshold of nitrogen input at which there is likely to be significant shift in ectomycorrhizal fungi diversity (5-10 kg N ha^{-1} yr^{-1}) [151]. Foliar sampling of pine trees in Thetford Forest has shown that, while some of the younger, actively growing trees in second planting rotations show nitrogen deficiency in needles, the majority of older trees have accumulated nitrogen in their needles to such an extent that nitrogen concentration is above the optimal level [152]. This may cause imbalances with other nutrients. The results from this study support and add to these observations. Although there was no significant difference between the nitrogen stock of the F, 0-5 cm and 10-20 cm layers (as a product of the layers' thickness), the litter and F layers had significantly higher total nitrogen concentration than the mineral soil layers (Figure 3.2). As with carbon, while there is some evidence that nitrogen is being incorporated into the uppermost soil layers (the 0-5 cm mineral layer had significantly higher total nitrogen concentration than the 5-10 cm and 10-20 cm layers), the majority of the high nitrogen input is clearly accumulating in the organic layers. In particular, the total nitrogen concentration of the F layer was more than five times greater than the 0-5 cm layer and almost 18 times greater than the 10-20 cm layer. In addition to the difficulty of incorporating nutrients into sandy soils, this could be due to nitrogen addition inhibiting litter decomposition, particularly in low litter quality (for example, where lignin content is high, such as conifer needles) [153].

These results have a range of important management implications. Low regional rainfall means that leaching is generally limited [148]. However, the sandy soil texture lends itself to extreme leaching events over prolonged wet periods. The accumulation of nitrogen could then lead to extremely high nitrate concentrations, with concerns for water quality issues (mean annual nitrate concentrations are three times the UK water drinking standard) [148]. Equally, disturbance of organic matter is likely to lead to mineralisation and associated long-term loss of nutrients from the system as it is not incorporated into the soil. Therefore, soil cultivation operations such as ploughing should be restricted as much as possible within the constraints of silvicultural objectives. As mineralisation and leaching is most likely after felling events due to a loss of canopy cover, it would also be advisable to leave areas fallow for as short a duration as possible and to schedule this for dry periods.

C:N ratio

Different tree species are known to influence the C:N ratio of soil through variability in the lignin and nitrogen content of their leaf litter [121,133,154]. The C:N ratio in the mineral soils was significantly lower in heathland sites than any management option that contained conifers (Figure 3.3). Furthermore, the C:N ratios of the mineral soil layers of pure broadleaved stands (monocultures and mixtures) was significantly lower than mixtures (where the primary component was conifer), and the means were universally lower than pure conifer stands (although not significant due to high variation). This confirms the trend increasingly reported in other studies that a higher C:N ratio in mineral soils is found under conifers than broadleaves [121,155]. This is attributed to higher foliar and litterfall C:N ratios in conifers compared to broadleaves, due to greater nitrogen use efficiency by conifers and thus lower nitrogen content in litter [155–157]; although there were not any significant pairwise differences in organic layers between management options, the mean C:N ratio of the litter layer was higher in conifers than broadleaves, supporting this hypothesis (see Appendix table B.4). Furthermore, less acidic soils under broadleaves will promote higher microbial diversity and more efficient nutrient cycling.

Ecosystem service indicators

Generally, higher total carbon and nitrogen concentrations and a lower C:N ratio are indicators of soil quality. Higher carbon stocks indicate greater carbon sequestration. In the organic soil samples, total carbon concentration was significantly higher in forested sites compared to heathland sites (Figure 3.2). Similarly, when both organic and mineral layers were included in the model, forest stands with conifers (either pure conifers or mixtures with broadleaves) had a higher mean carbon stock than broadleaved or open sites (although not significant at the Benjamini-Hochberg corrected significance level). In soil, carbon is present in different pools that have different turnover rates: a high proportion of carbon in the ‘active’ carbon pool indicates a biologically active soil, whereas more carbon in the ‘intermediate’ or ‘passive’ pools is better for carbon sequestration [158–161]. Different types of land use (e.g. grassland or forest) can alter the proportions of carbon in different pools, with implications for ecosystem services [158]. I did not measure this, but generally sandy soils are unable to hold much stable carbon, and given the low incorporation of carbon into the mineral layers, this is unlikely to be an important consideration in Thetford Forest.

Overall, combining the different ecosystem services indicators does not give a unified indication of soil quality as an ecosystem service. Forested sites had higher total carbon and nitrogen concentrations in the organic layers than heathland sites, although as discussed this is vulnerable to loss following forest operations disturbance, and there was no significant difference between management options in the mineral layers. Equally, it was not possible to detect a significant difference between management options for total plot carbon or nitrogen stock. Generally,

broadleaved stands and open sites had a lower C:N ratio, although only heathland had a significantly lower C:N ratio in the mineral layers than stands with conifers. Overall, the differences between management options are marginal, as the sandy texture and low quality of the soils is not amenable to change through land management. Therefore, forest land use choice does not have large effects on soil quality, which can be beneficial for commercial forestry (conifer monocultures, for example, are arguably no worse than broadleaves or open sites), but also constrains the capacity to deliver meaningful improvements to soil quality as an ecosystem service. In the Thetford Forest context, these results question widely held opinions that forestry (particularly broadleaves) will deliver soil quality and soil carbon sequestration gains.

4 | Long-term changes in soil pH in the Breckland region and the effects of afforestation

SUMMARY

It is widely acknowledged that afforestation affects soil pH, although this is variable by species and location. However, soil properties are not routinely monitored in commercial forestry, even though they are important factors in guiding future management strategies. The planting of Thetford Forest nearly 100 years ago represents an opportunity to study the long-term effects of afforestation on soil pH. I conducted a large soil sampling survey to explore how different forest management options and underlying soil types affect soil pH. I also compared my sampling results to historical records to determine how soil pH has changed over time. I found that soil pH was affected by management option, with conifers having a stronger acidifying effect than broadleaves. After the reversion of forested sites back to open habitat, pH recovered differently according to the historical soil type, with recovery of a pH akin to historically open sites on calcareous sites but not on acidic sites. These results have implications for conservation objectives and new planting strategies. Despite national trends of soil pH recovery following widespread acidification, I found strong evidence that the Breckland region is subject to ongoing acidification, likely to be caused by the high regional nitrogen emissions and deposition. The rapidity with which pH is changing may also make alternative forest management strategies, such as continuous-cover forestry and natural regeneration, much more appealing and effective than current forestry practices.

INTRODUCTION

Soil type is obviously crucial in deciding whether to afforest and, if so, which species to use. All tree species are adapted to a suite of ecological conditions, of which soil is of fundamental importance; the identification of forest soil types and selection of suitable tree species (alongside appropriate soil cultivation) is central to silviculture [95,162]. In turn, trees influence and modify a wide range of soil functions and properties [121,122,163–165]. Afforestation is well known to affect soil pH [166] but the effects of afforestation on soil pH vary by species. In general, forest soils tend to be more acidic than equivalent soils under grassland vegetation [135,167–169], which seems to be caused mainly through the redistribution of cations (increased cation uptake by trees causing localised acidification in the upper soil layers) [135,170]. Trees are also effective at scavenging atmospheric pollutants, leading

to increased deposition and acidification under forest canopies where aerial pollution is high [132,148,149]. Due to a greater canopy surface area and aerodynamic roughness, conifers scavenge atmospheric deposition more efficiently than broadleaved species [149,171,172]. Conifers also have a more acidic leaf litter than broadleaves. Taking these two factors together, conifers therefore tend to acidify soils more than broadleaved species [166,171]. A recent global meta-analysis found that afforestation with *Eucalyptus*, *Pinus*, and other conifers significantly decreased pH, while there was no change for other angiosperms [135]. The impact of afforestation on soil pH may also vary by location. A large study in China found that afforestation neutralises soil pH as it raises pH in acidic soil but lowers pH in alkaline soil [167]. Despite recognition of the fundamental importance of soil for forests, it is often not routinely monitored within the commercial forestry industry. Understanding the localised and specific impact of past management on soil properties is important for considering future management, so this represents a key opportunity for improvement.

In the UK, large areas of the country were afforested after the First World War with the creation of the Forestry Commission (tasked with generating a strategic timber reserve) [66]. Various forests are now approaching 100 years in age, representing an opportunity to study the long-term effects of afforestation on soil pH. Importantly, forest management rotations operate over long timescales with minimal or no soil inputs or cultivation. Therefore, natural soil processes continue beyond the initial afforestation and establishment period, and it is informative to explore to what extent soil changes continue to occur.

In particular, Thetford Forest (located in the Breckland region of East Anglia) is one of these 'new' forests and is an excellent site to study the effects of management on soils due to their highly variable nature across the landscape. Across Breckland, a combination of chalk-sand drift (with highly variable chalk content), sand and gravels, and wind-blown sand creates a mosaic of calcareous soils (where chalk is near the surface) and acidic soils (where there is deep sand over chalk) [57]. Although these historical spatial soil differences complicate the research plan and analysis, they can be incorporated into the study design to capture how afforestation and subsequent management differentially affect these soil types.

Historically there has been widespread soil acidification in the UK caused by extensive aerial pollution[173,174], but this is changing. Effective policy change has led to a dramatic decrease in atmospheric acid deposition, particularly of sulphur (reflected in the sulphate concentration in soils) [173–177]. There is now increasing evidence that the pH of UK soils is recovering [173,177,178]. However, the Breckland region has some of the highest dry deposition rates of ammonia in Great Britain, largely as a result of intensive pig and poultry farming in the region, and very high soil nitrate concentrations [175,179]. Recent transect studies at Thetford Forest have shown that localised nitrogen deposition can be up to four times as high as the critical load, which leads to soil acidification through nitrification [132,150]. This may counteract the positive effects of the reduction in other aerial

pollution, potentially not only preventing soil pH recovery but also leading to continued soil acidification. Given the general assumption that soils are generally recovering, this is particularly important to explore.

In this study, I firstly explore whether there are differences in present-day soil pH between different forest management scenarios – such as conifers, broadleaves, monocultures, mixtures – and historic heathland sites (which represent a non-afforested control). Secondly, I use historical records to determine how soil pH has changed over time, and how this is affected by land use.

METHODS

Plot selection

I selected forest plots to represent a variety of different land use and management options across the forest based on a GIS analysis. I used the soil map from the 1973 Breckland Soil Survey to ensure that both calcareous and acidic plots were identified for soil sampling for each management option (Table 4.1). Plots were only selected if the main tree or vegetation component was planted more than 15 years ago, to ensure that the crop was well established. Plots were selected that exceeded 2 ha (with the exception of one plot that was found to be sub-divided by species and therefore each section was smaller). The conifer monocultures comprised of Corsican pine, Scots pine, hybrid larch, Douglas fir or Weymouth pine. Species in broadleaved monocultures were sweet chestnut, eucalyptus, oak, beech and birch. Full information on the plots is given in Appendix table C.1.

Table 4.1: Summary of survey plots.

Management option	Category description	Calcareous plots	Acidic plots	Total number of plots
Conifer monoculture	One species, conifer	2	4	6
Conifer mixture	3+ species, all conifer	3	3	6
Broadleaved monoculture	One species, broadleaved	2	3	5
Broadleaved mixture	3+ species, all broadleaved	3	2	5
Mixture (primary conifer)	3+ species, combination of broadleaved and conifers, largest component is conifer	2	3	5
Mixture (primary broadleaved)	3+ species, combination of broadleaved and conifers, largest component is broadleaved	3	2	5
Open (cleared)	Sites recently cleared from forestry to revert to heathland (~15 years ago)	3	2	5
Heathland	Historical heathland sites, never planted	3	2	5
Total				42

Sampling procedure

Soil sampling took place in November and December 2016. At each plot, I selected three sub-plots by randomly generated coordinates. I collected samples from the organic and mineral layers (Figure 4.1). In forested sites, the organic layers were separated into the leaf litter layer (intact leaves or needles) and the fermentation (F) layer (partially broken-down leaf material and humus). In open sites, the organic layers also included a grass layer, but leaf litter was sometimes not present. The mineral layers were separated into three different depths below the F layer: 0-5 cm, 5-10 cm, 10-20 cm.

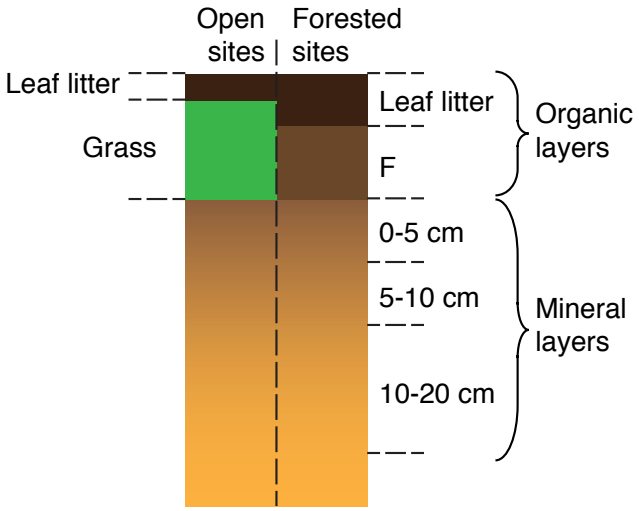

Figure 4.1: Diagram of soil layers sampled. The leaf litter and F layers may vary in depth.

At each sub-plot, I tapped down a 2-inch diameter soil corer until the top of the core was level with the top of the leaf litter (the full length of the soil corer including the nose was 35.5 cm). I collected mineral layers from the corer for all sites, and also the organic layers from the corer in open sites. In forested sites, I collected all organic layer material within a 25 x 25 cm quadrat adjacent to the corer. I recorded the time, date and GPS location of each sub-plot. I transferred samples to a fridge as soon as possible on the sampling day and stored them at 4°C until analysis.

Laboratory analysis

Samples were transferred to the Forest Research chemical laboratory at Alice Holt. Samples were oven-dried at 40°C and then individually sieved (2-mm) and milled. Soil pH (in water) was measured in each sample.

Historical data

There have been several soil studies in Breckland since the 1940s, exploring the soils of the heaths, grasslands, and later, the forest. To investigate the effects of afforestation on heathland sites, I compared my results to the available historical data on soils. I carried out extensive searches that uncovered six historical soil surveys from Thetford Forest (Table 4.2).

Table 4.2: Historical data sources of pH data in Thetford Forest region.

Source	Data description
Watt (1940)[180]	Grasslands classified from samples taken in Lakenheath Warren. Carbon and total nitrogen from composite samples of top 0-15 cm of soil from each grassland type given in a table. pH values for each grassland type at different depths represented in graph form only. Values were extracted from the graph using DataThief [181] .
Ovington (1953)[182]	pH measurements, *inter alia*, of 6 different plots in West Tofts (in north Thetford Forest).
Perrin (1955)[183]	Cambridge University thesis. Profile description, pH, organic carbon (%) (among other data) given for ten soil samples.
Corbett (1973)[57]	Breckland Soil Survey involved detailed mapping of the soil series found in the Breckland region. Grid reference and pH given for samples from each soil series. Organic carbon and nitrogen (%) also recorded for some of these samples. Survey published in 1973, but mapping took place up to 1963.
Howard & Howard (1984)[184]	Revisited Ovington [182] plots and re-took pH measurements.
Eycott (2006)[185]	pH data from top 0-5 cm of soil collected under Scots pine and Corsican pine stands around the forest.

To compare historical soil samples with present data, I grouped data according to soil series. Data collected in this study were collected on Worlington, Methwold, Santon and Freckenham soil series. Corbett is the first author to reference soil series, but through studying the approximate locations given by Watt and Perrin (Perrin also gives a soil genetic group), it was possible to work out which grassland types belonged to which soil series (see Appendix table C.2). I restricted pH data collected by Eycott[185] to include only compartments that were entirely within Methwold or Worlington soil series (according to the Corbett map [57]). I then categorised data from all studies according to whether it was collected on Methwold or Worlington soil series (or equivalent grassland types) and analysed the changes in pH for these different underlying soil types separately.

Data analysis

For each soil layer, I calculated the mean pH per plot from the values at each of the three sub-plots. For some leaf litter, F and grass samples there was insufficient material to accurately assess pH, so means were taken of the available data. I fitted a linear model with management option, soil layer

and historical soil type as predictors. I then separated data according to historical soil type (the broad soil type – either acidic or calcareous – as classified by Corbett in the Breckland Soil Survey [57]; it is important to note that these are relative terms), and fitted separate linear models for each (with management option and soil layer as predictors). I used a Type II ANOVA on the three linear models to determine which predictors were significant. Where predictors had a significant effect, I then used a Tukey-Kramer post-hoc test to find pairwise interactions that were significant. Before running the Tukey-Kramer I excluded all non-significant predictors from the model (at the 0.05 significance level).

To test whether there has been a change in pH over time, I used the data from grassland sites recorded by Watt (1940), Ovington (1953) and Perrin (1955) as baseline data. I grouped data from subsequent surveys according to their management option, and fitted a linear model using year and depth of the sample as predictors for pH and reported the significance value for year. Due to the lack of historical data on organic layers, I only included mineral soil data. Where historical pH was given for a range of depths (e.g. 0-5 cm), I used the median depth. I used the date of publication for each historical dataset as the year, unless the exact date was otherwise specified (Ovington: 1951, Howard & Howard: 1974, Eycott: 2001). For the Breckland Soil Survey sampling took place up to 1963, which I used as the year for the Corbett dataset.

To account for the possibility of increased type I errors through multiple testing of the same dataset, I used a Benjamini-Hochberg procedure to reduce the *P* value [141,142]. With a false discovery rate set at 5% the corrected significance *P* value was 0.023.

All data was analysed using R[143].

Difference in pH before and after drying

Some studies show that soil pH changes after drying [186,187] so this source of variation needs to be considered. It was not possible to determine from the historical studies whether pH was measured before or after soil drying, so I revisited and resampled several plots in June 2018 and measured pH before and after drying the soil in an oven. At each plot I selected three sub-plots by randomly generated coordinates. At the first sub-plot I took samples from each of the 0-5 cm, 5-10 cm and 10-20 cm layers; at the second and third sub-plot I took samples from the 0-5 cm layer only. On the same day, I transferred half of each soil sample to an oven (40^{o}C) for drying, and used the other half to measure the pH of the wet samples. When samples were completely dried (a few days later) they were removed from the oven and I measured the pH using a Hanna HI 98103 pH-meter. To analyse the difference in pH, I used a paired t-test. Two samples were mislabelled and excluded from the statistical test.

RESULTS

Difference between management options

Management option significantly affected pH, both when all plots were included and when data are subset by historical soil type (Table 4.3). Conifer monoculture had the smallest average pH (4.36) while heathland had the highest average pH (6.53) (Figure 4.2). Pure broadleaved stands (i.e. broadleaved monoculture or mixture) had higher average pH than pure conifer stands (i.e. conifer monoculture or mixture). Post-hoc Tukey-Kramer comparisons showed that conifer monoculture was significantly different to mixtures (where the primary component is broadleaved), broadleaved monoculture, broadleaved mixture, open (recently cleared) and heathland (unafforested) sites. In addition, heathland sites were significantly different to conifer monoculture, conifer mixture and mixtures (where the primary component is conifer). Overall variance is higher in calcareous plots.

Table 4.3: P values for the significance of predictors in all linear models. Green shading indicates significance.

Predictors / Data subset	Management option	Soil layer	Historical soil type
All plot types	<0.0001	0.4215	<0.0001
Only historically acidic plots	<0.0001	0.0017	NA
Only historically calcareous plots	0.0022	0.7434	NA

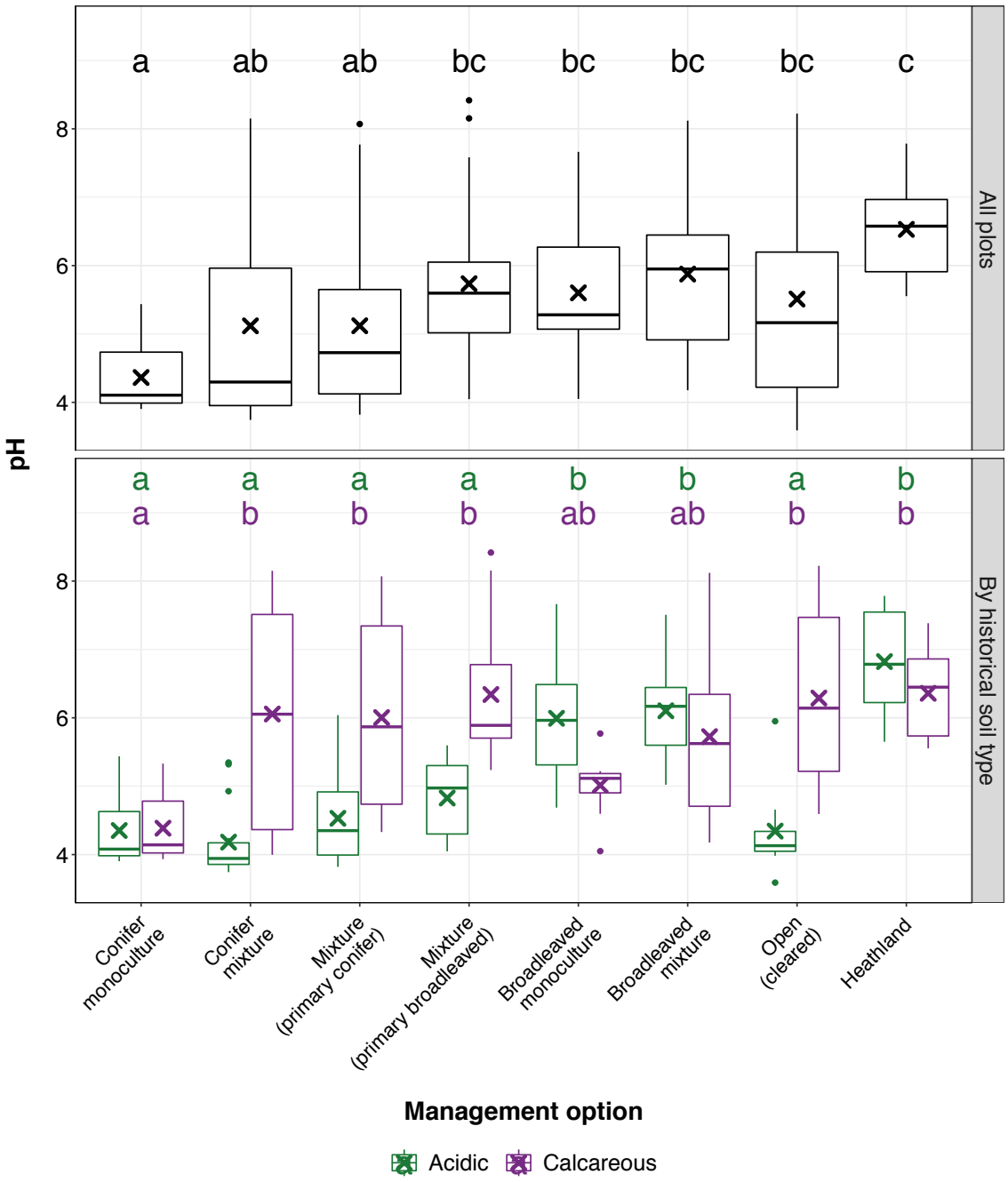

Figure 4.2: The pH of different management options. The top panel shows all data across all plot types, the bottom panel shows data separated by historical soil type. Boxplots with different letters indicate significant pairwise differences between management options (calculated using a Tukey-Kramer test); where boxplots share letters they are not significantly different at P = 0.05. Letter colours in the bottom panel indicate historical soil type; letters indicate differences between management options within each historical soil type, not differences between historical soil types. Crosses indicate the means. The bold horizontal line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles. Whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Points indicate values that are beyond the whiskers.

Change in pH over time

pH often declined over time. For data collected on Methwold sites (which are calcareous), year was a significant negative predictor of pH for conifer monoculture, broadleaved monoculture and heathland sites at the Benjamini-Hochberg corrected *P* value, and broadleaved mixture and open (cleared) sites at the traditional $P = 0.05$ significance threshold. For Worlington sites (which are acidic), year was also a significant negative predictor of pH for conifer monoculture and conifer mixture sites at the corrected *P* value, and mixtures (where the primary component is conifer) at the traditional significance threshold. The gradient over time was progressively less for each of these significant categories, when arranged in levels of decreasing conifer intensification and increasing broadleaved diversity (Figure 4.3). Significant regression lines are plotted in Figure 4.3.

Difference in pH before and after drying

Drying does not seem to be important to pH measurement. There was no difference in pH of samples before and after drying (paired t-test, $t = -0.52$, $df = 27$, $P = 0.6042$) (see Appendix figure C.1). The difference in means before and after drying was 0.03 (before: 4.72, after: 4.75). Given that there was no significant difference in pH before and after drying of samples, I can be confident that the change in pH over time observed in this study is not caused by methodological differences.

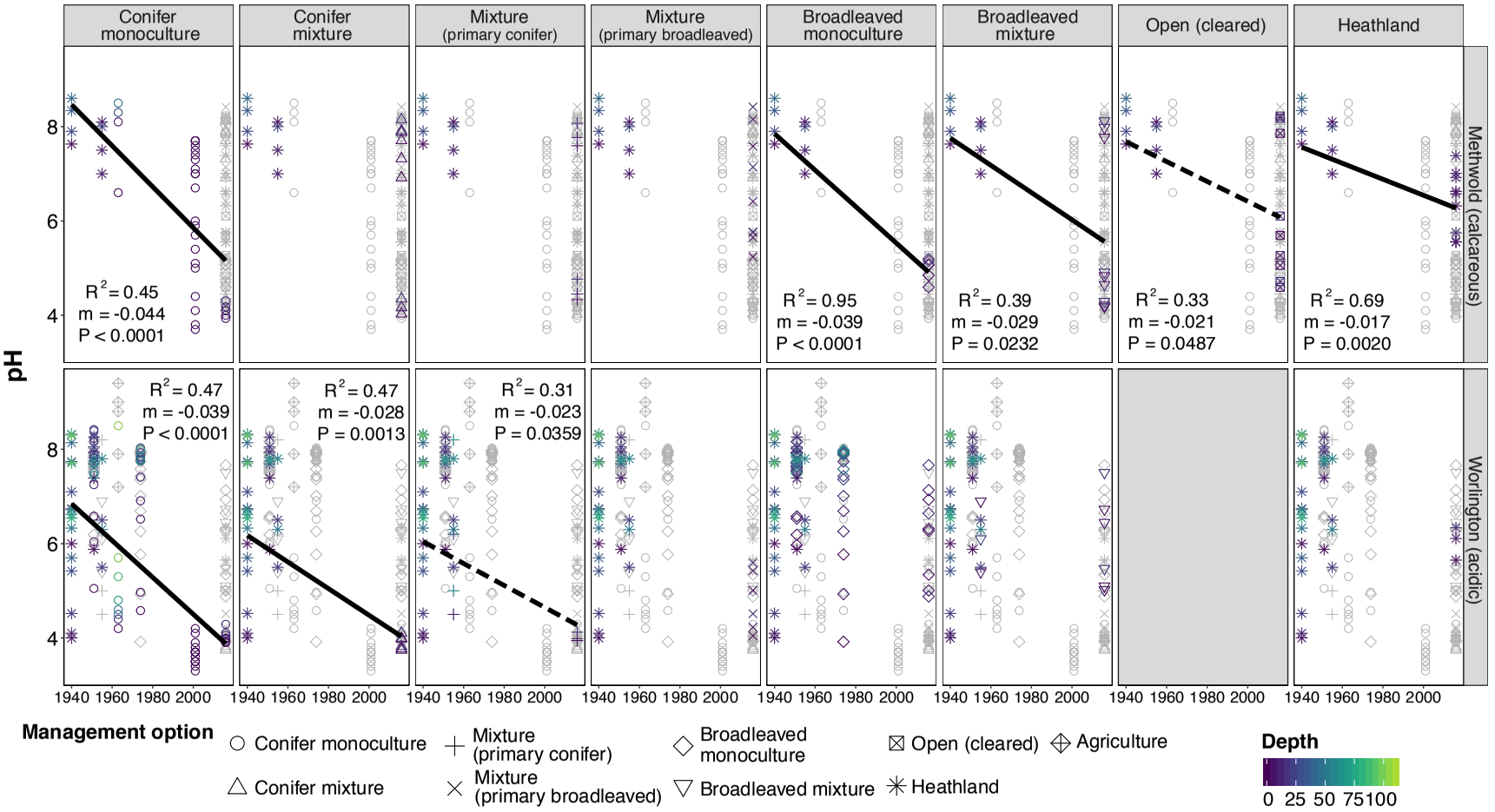

Figure 4.3: pH data points collected over time for Methwold (calcareous) and Worlington (acidic) sites. Grey symbols show all data collected for that historical soil type, coloured symbols highlight the data for respective management options and the grassland comparison data from 1940 and 1955. Colour of symbols indicate depth of mineral soil sample. Regression lines are plotted where year was a significant predictor of pH (and for illustration the line is drawn for a depth of 2.5 cm, which is the median of the most common sample, 0-5 cm). Lines are dashed where the P value is significant at the traditional P = 0.05 significance threshold, but not at the Benjamini-Hochberg corrected threshold. R^2 is variance explained by the line, m is the line gradient, P is the P value of the year predictor variable.

DISCUSSION

Difference between management options

Conifers reduced pH but this varied with soil type. The results from this study support the general observations that conifer afforestation lowers pH, as all sites managed as forest had a lower average pH than heathland sites that have always been open (Figure 4.2), but that broadleaved afforestation does not significantly lower pH [135,168]. Only sites that are entirely or mostly coniferous had a significantly lower pH than sites that have always been open. In Thetford Forest, the acidification effect is more pronounced on historically acidic sites where all sites with any conifer component, including mixtures with broadleaved species, had significantly lower pH than broadleaved or heathland sites. On historically calcareous sites only conifer monocultures had significantly lower pH than heathland sites. This is due to higher variance in the results of historically calcareous sites, which is to be expected as these sites have highly variable levels of chalk within the upper few metres of the soil, so pH is naturally very variable. Furthermore, potential pH decreases on these sites will be buffered by the neutralising capacity of the chalk.

Unlike other work I did not find a pH neutralisation effect of afforestation. Working in China, Hong et al.[167] found that following afforestation pH was lowered when control site pH was greater than 7, and raised when control site pH was lower than 5. I did not find a differential effect in this study, although sites classified as both historically acidic and historically calcareous had relatively high and variable pH (these classifications are based on historical studies and are relative to each other rather than being absolute). Therefore, it is probable that no sites were acidic enough to show an increase in pH through afforestation, as observed by Hong et al. [167].

Areas cleared of forest on chalk reverted to the pH of historically open habitat but this did not happen on acid sites. Sites that are recently open (i.e. cleared of forestry around 15 years ago) are part of a heathland reversion programme, which aims to restore habitats akin to sites that have always been open. Before clearance, these sites were planted with conifers (mainly monocultures). Within historically calcareous sites, the pH of recently open plots had recovered to pre-afforestation levels: pH was significantly higher than conifer monocultures, and no different to heathland plots (Figure 4.2). In contrast, within historically acidic sites, the pH of recently open plots had not recovered: pH was no different to conifer monocultures, but significantly lower than the plots that have always been open. During clearance of the sites, high disturbance and clearing of the organic layers would have caused acidification, through both nitrification (resulting in the release of H^+) and subsequent leaching of anions (nitrites, NO_2^-, and nitrates, NO_3^-) as water input increased due to loss of canopy cover [188].

On historically calcareous sites in Thetford Forest, high soil disturbance events, such as tree stump harvesting, have been observed to increase pH through disturbance of chalk [152]. This is therefore also likely to have occurred during the heathland reversion, leading to increased pH. A higher diversity and abundance of microorganisms in more alkaline soil types also leads to better nutrient cycling and soils are less prone to mineralisation and leaching events. In contrast, historically acidic sites would simply be exposed to further acidification through tree clearance.

Changes in pH are central to conservation management objectives. Both calcareous and acidic heathland have high biodiversity value – Breckland is designated as a Special Area of Conservation for its varied dry heaths [61,64] – and they support different plant communities. These results therefore have key management implications. Heathland reversion programmes must give careful consideration to the type of heathland that is being restored as site choice, soil type and clearance operations have a crucial influence.

Change in pH over time

Despite national decreases in atmospheric aerial pollution (and associated soil acidification) following effective policy change in recent decades, the Breckland region still has very high localised nitrogen deposition due to intensive regional agriculture [132,174,175,179]. The results from this study are strong evidence that the Breckland region is undergoing continuing dramatic acidification, in contrast to pH recovery more widely in the UK. Firstly, there was a significant decrease in pH over time on Methwold sites that have been always been open (i.e. heathland) (Figure 4.3). Secondly, there were also significant decreases in pH over time under pure broadleaved stands on Methwold sites, despite the fact that broadleaves would not generally be expected to decrease soil pH as much as conifers and national trends of increasing pH under broadleaved forest have been reported [118,139]. Thirdly, there were significant reductions in pH over time on calcareous (Methwold) sites, despite the neutralising capacity of calcium carbonate. Finally, conifer sites on historically acidic (Worlington) sites also showed a significant trend in decreasing pH over time (Figure 4.3). I did not find a significant relationship on Worlington sites with broadleaved components or open sites, most probably due to higher variation in pH of the reference grassland sites.

The greatest acidification has taken place under conifers, as demonstrated by the decrease in gradient of significant correlations from conifer monocultures and mixtures through to broadleaved and open sites (comparing gradients separately for Methwold and Worlington sites) (Figure 4.3). Additionally, a significant decrease in pH over time of conifer plots was observed on calcareous Worlington sites, but not broadleaved and open plots. This matches expectations: conifer tree canopies are more effective than broadleaves at scavenging atmospheric pollutants and have more acidic leaf litter than broadleaves [149].

The strength and rapidity with which the soil pH has changed since afforestation, particularly under conifer monoculture, may also make management through continuous-cover forestry and natural regeneration more appealing. Not only will this type of management favour mixtures, which are less acidifying than monocultures, but it will also allow those trees most suited to the local soil conditions to establish. Successful species choice would no longer be entirely dependent on the forester being able to accurately predict the variation in soil pH across the forest. Natural regeneration (i.e. self-seeding of tree crops) is likely to be particularly beneficial in Thetford Forest and similar regions due to the high spatial variation in the soils, particularly on historically calcareous soils.

5 | The effects of alternative land management options on water supply in a low rainfall environment

SUMMARY

Globally, forests are fundamental for the provision of water ecosystem services. Thetford Forest is widely recognised for its importance in the regulation of regional water quality, but its management will also have significant implications for the water supply for human use. In this chapter, I explore this by calculating the potential water use of different management scenarios and vegetation types. Heathland was by far the best scenario for water supply, whereas the overall water use of various forestry options was estimated to be above annual precipitation input. However, the overall water balance will be affected by the underlying soil types and aquifer properties, which will determine whether there is an overall recharge in winter months, or whether trees are able to access water in times of stress over the summer and thus lead to an overall deficit. The delicate balance between precipitation input and water use from forestry options will almost certainly be exacerbated in future with climate change. I predict that the consequences of this will vary spatially. Over sandy soil types, the viability of plantation forestry will be under threat as trees are unable to access belowground water; drought tolerance of commercial tree species will therefore be essential. Where chalk is close to the surface and vegetation can access belowground water, scenario choice may lead to conflict between forestry and the projected regional increase in water supply demand.

INTRODUCTION

Ecosystem services relating to water encompass all four of the widely used Millennium Ecosystem Assessment categories of ecosystem services: supporting (water cycling), provisioning (water supply), regulating (water purification and flood defence) and cultural (recreation and tourism) [1,2,189]. They are arguably some of the most important ecosystem services, being fundamental to human wellbeing (for example, universal access to safe water resources is one of the United Nations Sustainable Development Goals) [189,190]. Land use choice and management affects the delivery of all ecosystem services [4,9,25]; in particular, forests and woodlands are extremely important for the provision of water ecosystem services [191].

Thetford Forest is an important landscape for several water ecosystem services. The Thetford region receives some of the highest nitrogen deposition rates nationally, largely as a result of livestock

production [149,175,179]. Tree canopies (particularly conifers) are effective at scavenging pollutants, which can lead to enhanced deposition and water quality issues under forests [128]. In some areas under Thetford Forest, for example, dissolved nitrate levels are more than three times higher than the UK water drinking standard [148]. However, there is also very low precipitation input, which limits the capacity for leaching, so much of the pollutants accumulate in organic material. While this risks pulses of pollution entering the water system in prolonged wet weather, much of these pollutants would enter the local water system anyway (particularly given the highly reactive nature of ammonia, which is the key pollutant from local livestock). Much of the surrounding landscape is intensive agriculture, which is responsible for the heavy enrichment and eutrophication of freshwater across the UK [192,193]. The land use and management options under consideration in Thetford have no or negligible chemical inputs (herbicide is sometimes used when commercial forestry stands are first planted, but given the long rotation times this is marginal compared to agriculture). Therefore, Thetford Forest represents an extremely important landscape for the maintenance of regional water quality [65]. Nevertheless, due to the limited differences in consequences for water quality between management options, I do not analyse water quality issues in this chapter. Additionally, woodlands can be effective at preventing and alleviating flooding, particularly at a local level [128,194,195]. However, the Breckland landscape (encompassing the forest) is extremely flat, with freely draining, sandy soils, so currently flood management is not a consideration [56,57].

The most important water ecosystem service affected by the management of Thetford Forest is probably water supply for human use (a provisioning ecosystem service). Regionally, the landscape has very low precipitation input. However, there is high demand for water for drinking purposes and agricultural abstraction. Water abstraction from aquifers underneath the forest (particularly given their relative purity given the wider catchment-scale water issues from intensive agriculture) is vital in meeting the drinking water demand. Therefore, the rate of aquifer recharge is an important issue, which can be greatly affected by the overlying land management.

Water supply is likely to be even more significant in future in the Breckland region for several reasons. Climate change predictions are uncertain, but central estimates indicate an increase of 16% in winter precipitation and decrease of 14% in summer precipitation by the 2080s under a low emissions scenario [196]. A high emissions scenario gives a winter increase of 26% and summer decrease of 27% in precipitation. This is coupled with temperature rises of 2.6-4.5 °C [196]. Summer droughts will therefore become much more intense, and the winter recharge of aquifers will be crucial. Additionally, population growth will increase demand; Anglian Water forecast their region to include an extra 1 million people, with an associated increase in water demand of 10%, by 2045 [197]. Nationally, water abstraction for agriculture and spray irrigation represented only 0.7% of total abstraction in 2016 (the majority of abstractions were for public water supply and electricity

supply); however the proportion of these two types of abstraction was nearly five times greater in the wider Anglian region [198]. Groundwater abstraction for agriculture from the Great Ouse Chalk aquifer is over 10% of the total abstraction [199]. Moreover, models of UK demand for irrigation suggest that future irrigation growth is likely be concentrated in the Breckland and surrounding regions [200].

In this chapter, I use vegetation water use to calculate water supply to the catchment. Thetford Forest is located above a large chalk aquifer, and the overall hydrological cycling is complex, with significant variation in aquifer properties (such as transmissivity) over small areas as well as regionally [199,201,202]. However, to understand the impacts of different management options on water supply as an ecosystem service, it is sufficient to consider how different land use options use water and ultimately how much water is prevented from entering, or is extracted, from the overall hydrological cycle. In general, trees use more water than other vegetation, and conifers use more water than broadleaves [128,203]. Many studies exploring water use in commercial conifer forests have focused on the uplands, which have quite different climates to Thetford Forest (notably much greater precipitation) [128,204]. However, large scale conifer forests pose the greatest risk to water supply if in dry, lowland regions [128,204]. Given the unusual climate of the Breckland region (being both warm and dry), I calculate the potential water use of different management options by developing and parameterising water use models with local climatic data and land management information. I also compare the effects of different climates in forestry locations across the UK, and explore the relative importance of different climatic variables in determining overall water loss from different management categories. Finally, I use climate change predictions to assess how water use might change in future. These analyses illustrate the key considerations in the future management of Thetford Forest to ensure the continued delivery of water supply.

METHODS

Development of a water loss model

To estimate water loss from different scenarios I adapted the Calder-Newson model of annual evaporation [205]. The Calder-Newson model estimates the evaporation loss of a forested catchment by dividing the area into forested (i.e. complete canopy coverage) and non-forested areas. In the forested areas, the evapotranspiration rate is multiplied by the proportion of time when the canopy is dry (as evapotranspiration does not occur when the canopy is wet). This is then added to an annual interception rate of the canopy (the annual precipitation multiplied by the interception fraction of the canopy). In the non-forested areas, a simple evapotranspiration rate is calculated. The Calder Newson equation is therefore [205]:

$$E = [(1 - f) \times E_t] + f[(1 - w)E_t + P\alpha] \quad (1)$$

where,

E = Annual evaporation

f = fraction of catchment area with complete canopy coverage

E_t = Penman evapotranspiration estimate of grass

w = fraction of year canopy is wet

P = annual precipitation (mm)

α = interception fraction

In upland areas of spruce forest, Calder & Newson (1979) [205] concluded that the reference Penman evapotranspiration estimate of grass was an approximate estimate for the evapotranspiration from the forest [205]. However, they recommended that the different transpiration characteristics of grass and forest vegetation be taken into account in drier lowland areas, as overall interception loss would be much smaller and therefore differences more difficult to detect. I therefore elaborated the Calder-Newson model to separate the evapotranspiration components of the different vegetation types:

$$E = \left[(1 - f) \times E_g\right] + f\left[(1 - w)E_f + P\alpha\right] \quad (2)$$

where,

E_g = Evapotranspiration estimate of alternative land cover (grass)

E_f = Evapotranspiration estimate of forest vegetation

In the Thetford Forest region, the non-forested areas (denoted by $(1 - f)$) are likely to be rough grassland typical of the heathland areas. Therefore, I defined E_g as the evapotranspiration estimate of rough grassland.

Whereas the interception loss of short grass crops (such as that defined by the reference Penman evapotranspiration estimate) is considered to be negligible due to low aerodynamic roughness [204], taller vegetation cover, such as rough grassland or heathland, will contribute an interception loss (albeit a lower one than under forest). Therefore, I incorporated this into the annual evaporation model:

$$E = (1 - f)\left[(1 - w)E_g + P\alpha_g\right] + f\left[(1 - w)E_f + P\alpha_f\right] \quad (3)$$

where,

α_g = interception fraction of rough grassland

α_f = interception fraction of forest vegetation

To account for seasonal differences in vegetation characteristics, I calculated water loss monthly rather than annually. For broadleaved trees, there is no evapotranspiration contribution in months where the canopy is leafless, so for the months of November to April (inclusive), the assumption is that $E_f = 0$.

Therefore, the final equation for annual water loss for forested scenarios was as follows:

$$E = (1 - f)\left[\sum_{m12}^{m1}(1 - w)E_g + P\alpha_g\right] + f\left[\sum_{m12}^{m1}(1 - w)E_f + P\alpha_f\right] \quad (4)$$

where,

m = month

For heathland (equivalent to grassland), $f = 0$; therefore:

$$E = \sum_{m12}^{m1}(1 - w)E_g + P\alpha_g \quad (5)$$

Calculation of parameters

I followed the formulae set out in Calder & Newson (1979) [205] to estimate w, and used f = 0.67 following Calder (2003) [206].

α (interception fraction)

The interception fraction of trees is well-established, decreasing with increasing annual precipitation. The interception fraction of broadleaved trees is lower than that of conifers. The mean annual rainfall of the Thetford Forest region (all 5km grids covering some part of the forest) is 638.3 mm [207]. Interception ratios were therefore estimated as 0.21 (broadleaves) and 0.42 (conifers), estimated from Figure 2 in Nisbet [204] using WebPlotDigitizer [208].

Interception rates of grassland are relatively understudied and uncertain compared to tree canopies. The literature reports highly variable rates of interception loss, from around 5% [209] to 100% [210,211]. Where there is little, low intensity precipitation, interception loss is expected to be high in

grasslands (as opposed to high rainfall intensity, where water reaches the ground more quickly) [211]. The daily precipitation average (calculated as monthly rainfall/ number of days > 1mm rain) in the Thetford Forest region is 4.2-6.9 mm (average per month); the average rainfall intensity is 5.0 mm/h [207]. Based on the little available literature on the interception ratios of grasses (see Appendix table D.1), I used an interception ratio of 0.1 for rough grassland.

P (annual precipitation)

I used monthly data of rainfall (mm) and yearly averages of rainfall intensity (mm/hour) from the UKCP09 Met Office 5km gridded datasets [207]. I took averages of the latest 10 years of available data (rainfall: 2007-2016; rainfall intensity: 2005-2014). Rainfall data were averaged for each month, rainfall intensity data were averaged over the 10 years. To calculate monthly rainfall hours (to enable calculation of w), I divided the monthly average of precipitation by the annual average rainfall intensity.

Evapotranspiration estimates

I used the Penman-Monteith evapotranspiration equation, which is widely used, and the FAO standard for calculating crop and reference (grass) evapotranspiration [212]:

$$\lambda ET = \frac{\Delta(R_n - G) + \rho_a c_p \frac{(e_s - e_a)}{r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)} \text{ MJ m}^2\text{day}^{-1} \quad (6)$$

where,

R_n = the net radiation (MJ m^{-2} day^{-1})

G = the soil heat flux (MJ m^{-2} day^{-1})

$(e_s - e_a)$ = the vapour pressure deficit of the air (kPa)

ρ_a = the mean air density at constant pressure (kg m^{-3})

c_p = the specific heat of the air (MJ kg^{-1} $^oC^{-1}$)

Δ = the slope of the saturation vapour pressure temperature relationship (kPa $^oC^{-1}$)

γ = the psychrometric constant (kPa $^oC^{-1}$)

r_s = (bulk) surface resistance (s m^{-1})

r_a = (bulk) aerodynamic resistance (s m^{-1})

I simplified the standard equation using constant values, following the FAO guidance for a grass reference crop [212], although retaining the r_s term so that I could adapt the equation for different vegetation. The full workings of this are outlined in Appendix D. This gave:

$$\lambda ET = \frac{\Delta(R_n - G) + \frac{2.1457\gamma\lambda \times (e_s - e_a)}{(T + 273) \times r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)} \quad (7)$$

where,

T = temperature (°C)

λ = latent heat of vaporisation (2.45 MJ kg^{-1})

Standardisation of units

As each component in the equation (7) is measured in different units, I had to multiply certain components by 86400 (to convert from seconds to a day), and then further divide by λ to convert MJ m^{-2} day^{-1} to mm day^{-1}. The full workings are outlined in Appendix D. This gave a final evapotranspiration formula:

$$ET = \frac{0.408\Delta(R_n - G) + \frac{86400 \times 2.1457\gamma \times (e_s - e_a)}{(T + 273) \times r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)} \text{ mm day}^{-1} \quad (8)$$

Calculation of parameters

I followed the FAO guidance for the calculation of the Δ, R_n, G, e_s, and γ parameters (see Appendix D) [212]. Monthly estimates of hours of sunshine, mean temperature, vapour pressure, maximum temperature, and minimum temperature were downloaded from the UKCP09 Met Office 5km gridded datasets [207]. As with rainfall data, I took monthly averages of the latest 10 years of available data (hours of sunshine, maximum temperature, minimum temperature, mean temperature: 2007-2016; vapour pressure: 2005-2014). I calculated the mean elevation for each 5km grid square from the Ordnance Survey Terrain 5 DTM land and height data [213].

For the calculation of R_n, I used an albedo value of 0.23 (the grass reference value), the recommended values for a_s and b_s ($a_s = 0.25$ and $b_s = 0.5$), and values of R_a (extraterrestrial radiation) and N (maximum possible sunshine hours) from the lookup tables in Annex 2 of the FAO guidance [212]. As Thetford Forest is near sea level (mean elevation of 30.5m), I used equation 37 of the FAO guidance [212] to estimate clear-sky radiation ($[R_{so} = (0.75 + 2 \times 10^{-5} \times z) \times R_a]$, where z is elevation).

Aerodynamic resistance

Due to a lack of data measuring wind speed and humidity directly over the forest canopy, I calculated aerodynamic resistance for a dry canopy using the equations and parameters set out in Mu et al. (2011) [214] and explained in detail in Appendix D. The overall estimate of evapotranspiration is insensitive to the value of aerodynamic resistance, and so such an estimate was deemed appropriate [215,216]. Ershadi et al. [217] tested different methods of parameterisations of evapotranspiration models, and found that parameterisation of aerodynamic resistance by the Mu [214] method performed better than parametrisation following Thom [218] (the default for the FAO methodology) for broadleaved forests, and was not considerably worse for conifer forests

(comparing scenarios of the Penman Monteith evapotranspiration model where only the aerodynamic resistance parameterisation varies) [217].

Due to relatively high variation in temperature, aerodynamic resistance fluctuates seasonally (Figure 5.1 and Table 5.1). In the summer months the value is low (close to the low values of aerodynamic resistance often reported in the literature, e.g. 5 s m^{-1} [215]), whereas the winter months have a much higher resistance.

Table 5.1: Summary statistics for monthly aerodynamic resistance of different scenarios.

Scenario	Mean	SD	Min	Max
Broadleaved	12.6	14.5	1.0	37.9
Conifer	7.2	6.7	1.0	17.7
Heath	9.9	10.5	1.0	27.5

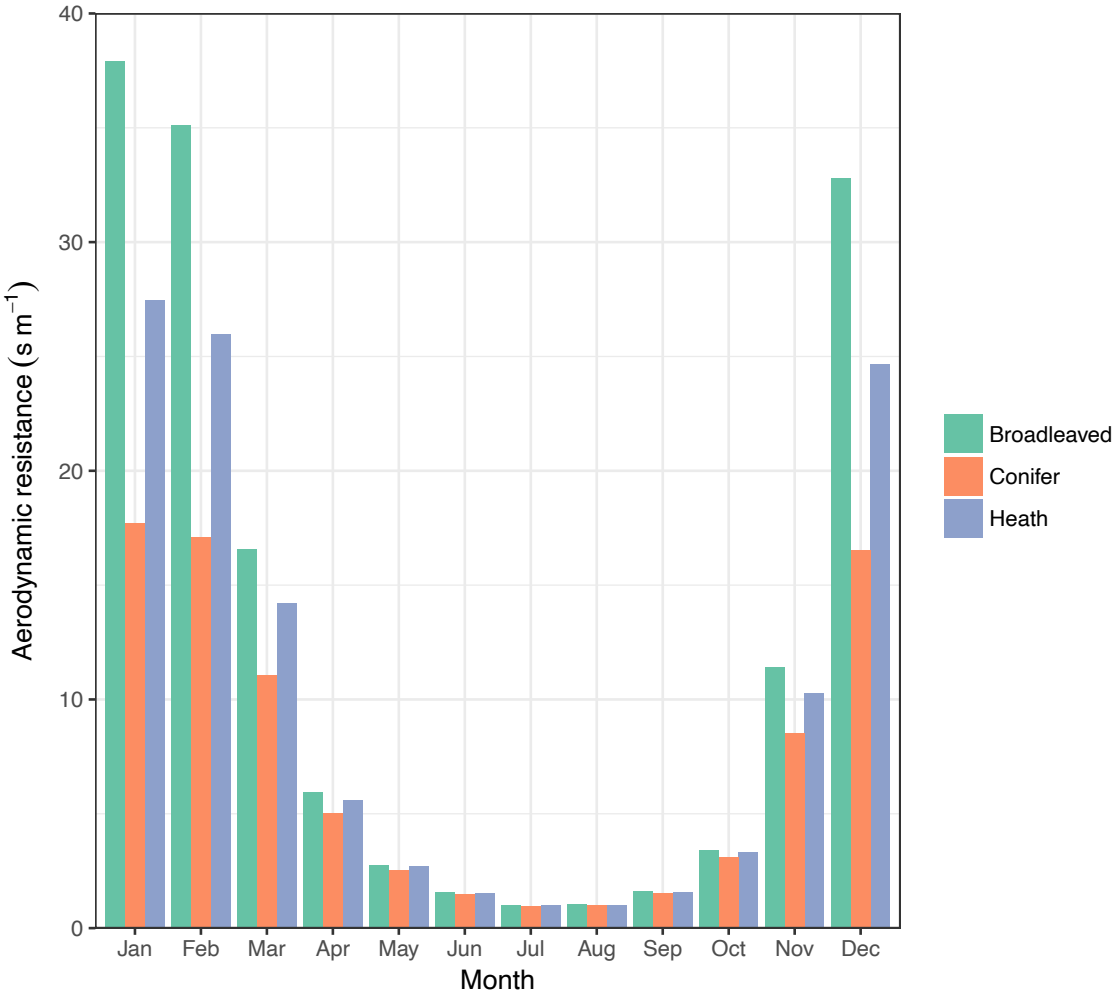

Figure 5.1: Monthly fluctuations of the aerodynamic resistance of different scenarios.

Surface resistance

I incorporated the effects of different vegetation characteristics on evapotranspiration by calculating the surface resistance for different types of vegetation.

$$r_s = \frac{r_l}{LAI_{\text{active}}} \tag{9}$$

where,

r_s = (bulk) surface resistance (s m^{-1})

r_l = (bulk) stomatal resistance (s m^{-1})

LAI_{active} = active leaf area index (m^2 m^{-2})

$$LAI_{\text{active}} = 0.5 \times LAI \tag{10}$$

where,

LAI_{active} = active leaf area index (m^2 m^{-2})

LAI = leaf area index (m^2 m^{-2})

I searched the literature to find as many values as possible for the stomatal resistance and the leaf area index of species included in different scenarios, as follows. Conifer and broadleaved tree species included any tree species currently present in Thetford Forest. Heathland species were defined as those species that are present in the NVC communities of Breckland SSSIs containing grass-heath (as specified in Table 5, Dolman et al. [2010] [61]). Species in each NVC community are specified in floristic tables [219]; I used species that had a constancy value of IV or V (i.e. are highly likely to be present).

Data extracted from papers were normally controls from experiments, being the value of conductance or resistance under normal ambient conditions. Where data were presented on graphs, I extracted values using the programme WebPlotDigitizer [208]. To account for potential inaccuracies in extracting the data this way, I rounded values to a sensible threshold depending on the units (1 decimal place: resistance was measured in s cm^{-1}; 3 decimal places: mol m^{-2} s^{-1}; whole number: mmol m^{-2} s^{-1}). I converted values of stomatal conductance to resistance by taking the inverse. Where values were reported in molar values, I converted to units of m s^{-1} by division with a constant determined by ideal gas laws (I assumed the standard pressure of 1 Pa for all sites, and unless otherwise reported, a standard temperature of 25°C).

There is high diurnal variation in stomatal resistance, with resistance increasing in the evening and early morning. Different papers reported values across different times (see Appendix table D.2); sometimes data from all times were reported whereas in others only the overall mean across the day was reported. As means were skewed according to whether values into the evening were reported,

I set a lower and upper time cut-off at 6h and 17h respectively (the earliest and latest times that data were collected when only an overall mean was reported).

In addition to data gathered from the literature, I also used data from the TRY database [220]. I used stomatal conductance data (data name: stomatal conductance to water vapour per leaf area) that was a mean (rather than maximal). As there was a high number of data points, I restricted heath species to those within Europe. This resulted in a total of 6 datasets [221–228].

All stomatal resistance data are summarised in Table 5.2. Due to a high right skew in the data, I took the median value.

*Table 5.2: Summary statistics for each scenario/species. Stomatal resistance and leaf area index values collected from the literature. Surface resistance calculated using median stomatal resistance and mean leaf area index (0.5*LAI).*

Scenario/species	Stomatal resistance (s/m)				Leaf area index			Surface resistance (s/m)
	n	Mean	SD	Median	n	Mean	SD	
Conifer group	23	403.2	239.4	**325.8**	222	**5.43**	3.40	120.1
Norway spruce					94	**7.28**	3.36	61.6
Scots pine					106	**3.83**	2.55	170.4
Broadleaved group	46	343.6	509.3	**224.4**	237	**5.13**	2.05	87.4
Beech					149	**5.85**	1.94	76.7
Birch					34	**3.11**	1.16	144.3
Oak					24	**4.62**	1.54	141.2
Heath	176	425.5	450.4	**289.6**	27	**1.83**	1.23	316.2

I used the global LAI woody plants database to extract leaf area index values for trees (species selection was the same as for stomatal resistance, and data were restricted to within Europe) [229]. I aggregated data by broadleaved or conifer. Additionally, I separated leaf area index by species where there were at least 20 data points (Table 5.2), which enabled calculation of evapotranspiration by species (the stomatal resistance data was the same for either broadleaved or conifer species, as there were not enough observations to separate out) – Scots pine, Norway spruce *Picea abies*, birch, beech, oak. For heath species, I used leaf area index data from the LAI global plant database [230]. As there was a low number of measurements for grassland species (and there were no measurements for the species in the Breckland heaths), I used all data that was defined as in a grassland biome (and subset to within Europe or the USA). This is summarised in Table 5.2.

Total values calculated for surface resistance are given in Table 5.2.

Total water loss in Thetford Forest

I calculated the total water loss using equations 4 and 5 for each scenario: conifer, broadleaved, Scots pine, Norway spruce, birch, beech, oak, and heath. I separated this total value into interception and potential evapotranspiration components. In addition to calculating annual totals, I calculated

interception and potential evapotranspiration, and precipitation minus total potential water loss (i.e. potential recharge or deficit), per month for both Scots pine and Norway spruce scenarios.

Checking estimates

To validate my estimates using these models, I compared my calculations for Scots pine against the reported values by Gash & Stewart (1977) [215]. Gash & Stewart estimated transpiration from a Scots pine stand in Thetford Forest in 1975 using site-specific values of surface and aerodynamic resistance and weather measurements from a tower mounted above the stand [215,231,232]. Gash & Stewart used a correction factor to account for transpiration being reduced to 0 when the canopy is wet; I calculated the uncorrected values (i.e. transpiration + 0.07*interception), which were the outputs from their calculations using the Penman-Monteith evapotranspiration model. I calculated an equivalent evapotranspiration rate using my Scots pine parameters and using weather data from 1975 (UKCP09 Met Office 5km gridded datasets [207]). To enable comparison to the values from Gash & Stewart, I did not account for periods of canopy wetness and simply multiplied up my daily rate to find monthly totals. As the values from Gash & Stewart were presented for four-weekly intervals rather than by month, I compared cumulative transpiration curves over the year. I also tested whether there was a significant difference using a Type II ANOVA (with dataset and day as predictors).

I then used my full water loss model to find an overall figure for water loss rate from the catchment (equation 4). The reported annual precipitation value of 595.1 mm reported by Gash & Stewart (1977) [215] is substantially higher than the mean annual precipitation calculated across the forest landscape using the UKCP09 Met Office gridded data, which is 545.3 mm. I therefore used the values from Gash & Stewart to calculate the interception contribution using my model ($(1-f)\left[P\alpha_g\right] + f\left[P\alpha_f\right]$ components of equation 4).

Total volume calculation

To calculate the total volume of water loss, I converted the annual evapotranspiration total (mm $year^{-1}$) to a volume per hectare (m^3 ha^{-1} $year^{-1}$) by multiplying by a factor of 10 [212]. I calculated a total value separately for each 5km grid square (due to slight differences in climatic variables from the Met Office data). To calculate the total volume over the forest area, I multiplied the total from each 5km grid square by the area of forest in each grid square. I calculated the total rainfall across the forest in the same way. I then subtracted the total water loss from each scenario from the total rainfall to find the deficit total. Total volume was calculated for the different forestry scenarios (Table 5.2).

Water loss in different locations

I ran the analysis for different forestry locations in the UK, in order to assess the effect of different climatic variables on water loss from forestry. I changed the interception ratio according to the mean annual precipitation (Kielder: broadleaves α = 0.18, conifers α = 0.36, Dean: broadleaves α = 0.19, conifers α = 0.38) [204].

Effects of climatic variables on water loss

Rainfall

To explore the effects of rainfall on total water loss, I simulated the addition of extra rainfall to the Thetford Forest region (in 5 mm increments), while maintaining a constant evapotranspiration rate. Higher rainfall resulted in higher wet canopy time (w). In reality, increased rainfall is likely to also result in reduced temperature and sunshine hours, although I did not account for this.

Other climatic variables

I altered the values of a range of climatic variables and parameters (maximum temperature, mean temperature, minimum temperature, hours of sunshine, vapour pressure, elevation) in order to determine the relative effects of these variables on the evapotranspiration rate. I used the climatic values for Thetford as the baseline and simulated a 50% increase and decrease in each climatic variable. I then calculated the evapotranspiration rate for each different value for each variable, while keeping the other variable values constant at the Thetford baseline norm. I also calculated the average percentage difference of each variable in Kielder and the Forest of Dean from the Thetford value, and again calculated the evapotranspiration rate for each change in variable while keeping the other variables constant. Of course, this does not account for interactive effects. For each calculation, I used conifers as the vegetation scenario.

To explore the variation in evapotranspiration estimates as a result of variation in climatic variables across the Thetford Forest region, I calculated which 5km grid square had the highest and lowest total annual evapotranspiration ($\sum_{m12}^{m1}(1-w)E_f$) for Scots pine. I then calculated evapotranspiration rate using different combinations of weather variables, as outlined in Table 5.3, to explore which weather variables had the greatest effect on influencing evapotranspiration rate.

Table 5.3: Weather variables changed for each scenario. When using the maximum 5km square weather variables as default, the corresponding minimum 5km square weather variables was substituted in for each scenario, and vice versa.

Scenario	Weather variable changed
0	None
1	Sunshine hours
2	Maximum temperature
3	Minimum temperature
4	Mean temperature
5	Vapour pressure

Climate change predictions

Finally, I used climate change predictions to calculate interception and evapotranspiration rates of Scots pine for the 2080s, under a low emissions scenario. I used monthly mean, maximum and minimum air temperatures and average relative humidity (at 1.5 m height) and precipitation rate for the 25km squares that cover Thetford Forest (grid cells 1475 and 1514), downloaded from the UKCP09 User Interface. Values used were from the 50% probability level of climate change predictions. I averaged the current values of sunshine hours and elevation across the entire forest and used the same values for both grid cells. I also used the average present-day precipitation intensity to estimate total rainfall hours (as there are only predictions for precipitation per day). There are no predicted values of vapour pressure, so I calculated actual vapour pressure using relative humidity and temperature values:

$$e_a = \frac{RH_{mean}}{100}\left[\frac{e^o(T_{max}) + e^o(T_{min})}{2}\right]$$

where,

e_a = actual vapour pressure (kPa)

RH_{mean} = mean relative humidity

$e^o(T)$ = saturation vapour pressure at temperature T

However, calculating vapour pressure in this way gives different evapotranspiration values to using vapour pressure values directly, as I have calculated for present-day climatic variables. Exploration of data using present-day downloaded data showed that using relative humidity decreased evapotranspiration rates by around 15% compared to using vapour pressure values directly. To enable comparison to other calculations in this chapter, I therefore multiplied evapotranspiration rates by 1.18 (the mean percentage difference between calculations using relative humidity and vapour pressure). Testing this on present-day climatic variable data gave total evapotranspiration

loss values to within 2% of the original rates. I calculated evapotranspiration and interception for both Scots pine and heathland land uses, so that I could calculate a total water loss for a Scots pine scenario (equation 4). I calculated evapotranspiration and interception rates separately for each grid cell, and then averaged the monthly values. I calculated the water balance components per month and then calculated the difference between the precipitation and water loss.

Mean annual precipitation was 605.3 mm. I estimated interception ratios from Figure 2 in Nisbet [204]; given the small difference in total annual precipitation they were the same as present-day data (broadleaves: 0.21; conifers: 0.42).

Terminology

The Penman-Monteith model calculates potential evapotranspiration rate, rather than a true value. In reality, evapotranspiration is likely to be lower than this, especially in dry environments where plants come under water stress. From henceforth, I therefore refer to my evapotranspiration estimates as potential evapotranspiration, total water loss as potential water loss, and deficits (rainfall input minus potential water loss) as potential deficits. Similarly, calculated recharge values may be higher than reported.

RESULTS

Total water loss in Thetford Forest

I found that conifers had the highest total potential water loss (698.8 mm/year), followed by broadleaved trees (604.6 mm/year). Heathland had a much lower total potential water loss (310.8 mm/year) (Figure 5.2a). The broadleaved group had a higher potential evapotranspiration rate than the conifer group (Table 5.4). However, as broadleaved trees have seasonal leaf cover and therefore only transpire for part of the year, total potential evapotranspiration contribution is comparable to conifers (Figure 5.2a). The difference in total potential water loss between conifers and broadleaves arose from the higher interception rate of conifers (again, due to the seasonality of broadleaved canopy cover) (Figure 5.2a).

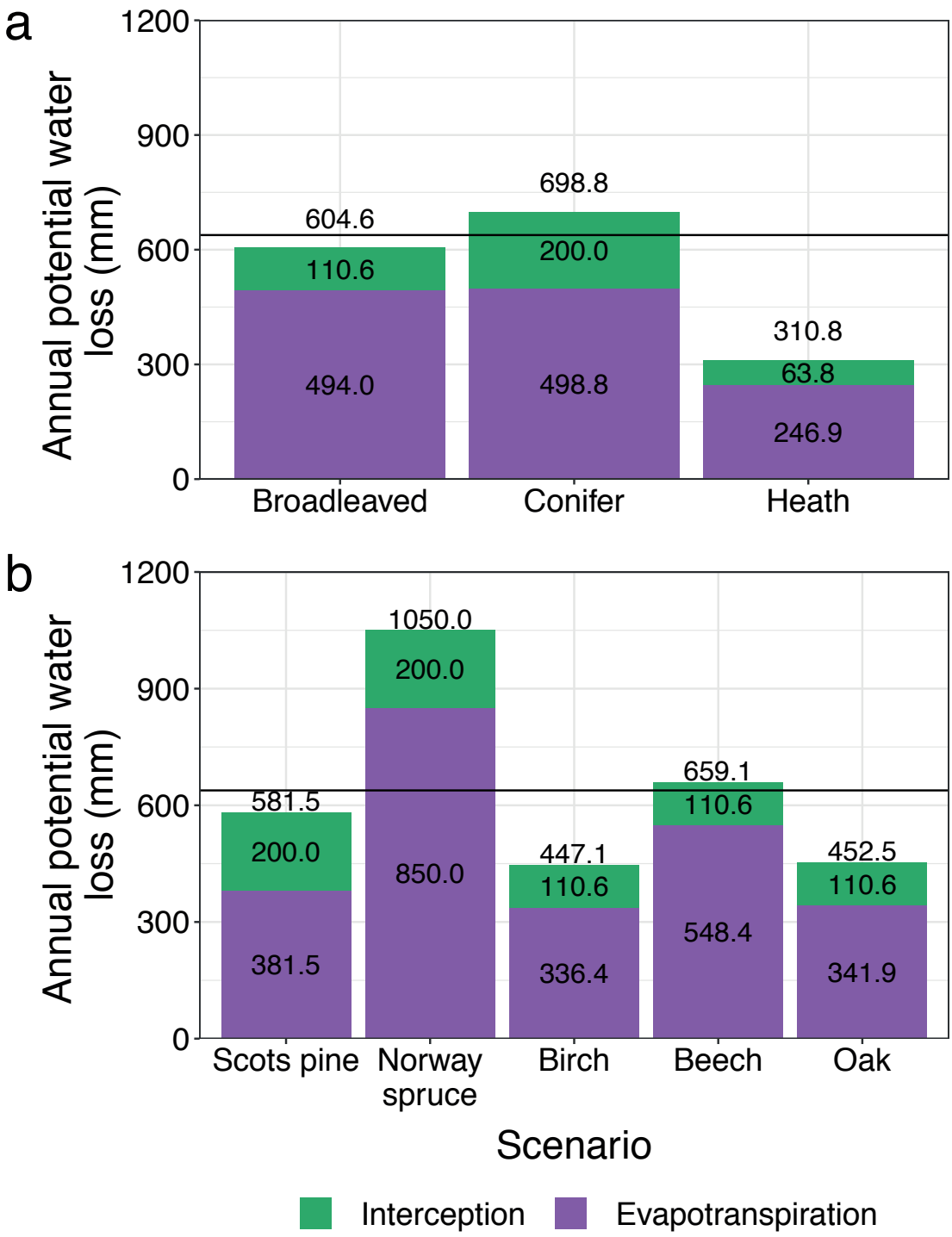

Figure 5.2: The total annual potential water loss of a) broad scenarios, b) individual species. Annual potential water loss for individual species was calculated when there were at least 20 data points per species for leaf area index values. The horizontal line represents the average annual precipitation of the Thetford Forest region.

Table 5.4: Mean potential evapotranspiration rates and the ratio of total water loss to annual rainfall for all scenarios.

Scenario	Group	Mean evapotranspiration (mm/day)	Rainfall ratio (water loss / annual rainfall)
Broadleaved group	Broad group	2.29	0.95
Conifer group	Broad group	1.74	1.09
Heath	Broad group	0.69	0.49
Beech	Broadleaved species	2.58	1.03
Birch	Broadleaved species	1.45	0.70
Oak	Broadleaved species	1.48	0.71
Norway spruce	Conifer species	3.21	1.65
Scots pine	Conifer species	1.25	0.91

There was great variation in the estimated total potential water loss for different tree species, including within conifers and within broadleaves (Figure 5.2b). Birch and oak had very similar potential evapotranspiration rates, whereas the potential evapotranspiration rate for beech was higher than Scots pine (Figure 5.2b). Norway spruce had the highest potential evapotranspiration rate, which was more than twice the rate of Scots pine. Conifers, Norway spruce and beech had an annual total potential water loss higher than annual precipitation input (Table 5.4; Figure 5.2).

The total water loss from potential evapotranspiration and interception exceeded precipitation input between April and September for Scots pine, and between March and October for Norway spruce (Figure 5.3). The deficit was much greater for Norway spruce than Scots pine over the summer months; in July, the potential evapotranspiration rate of Norway spruce was over three times the precipitation input that remained after interception was accounted for (Figure 5.3).

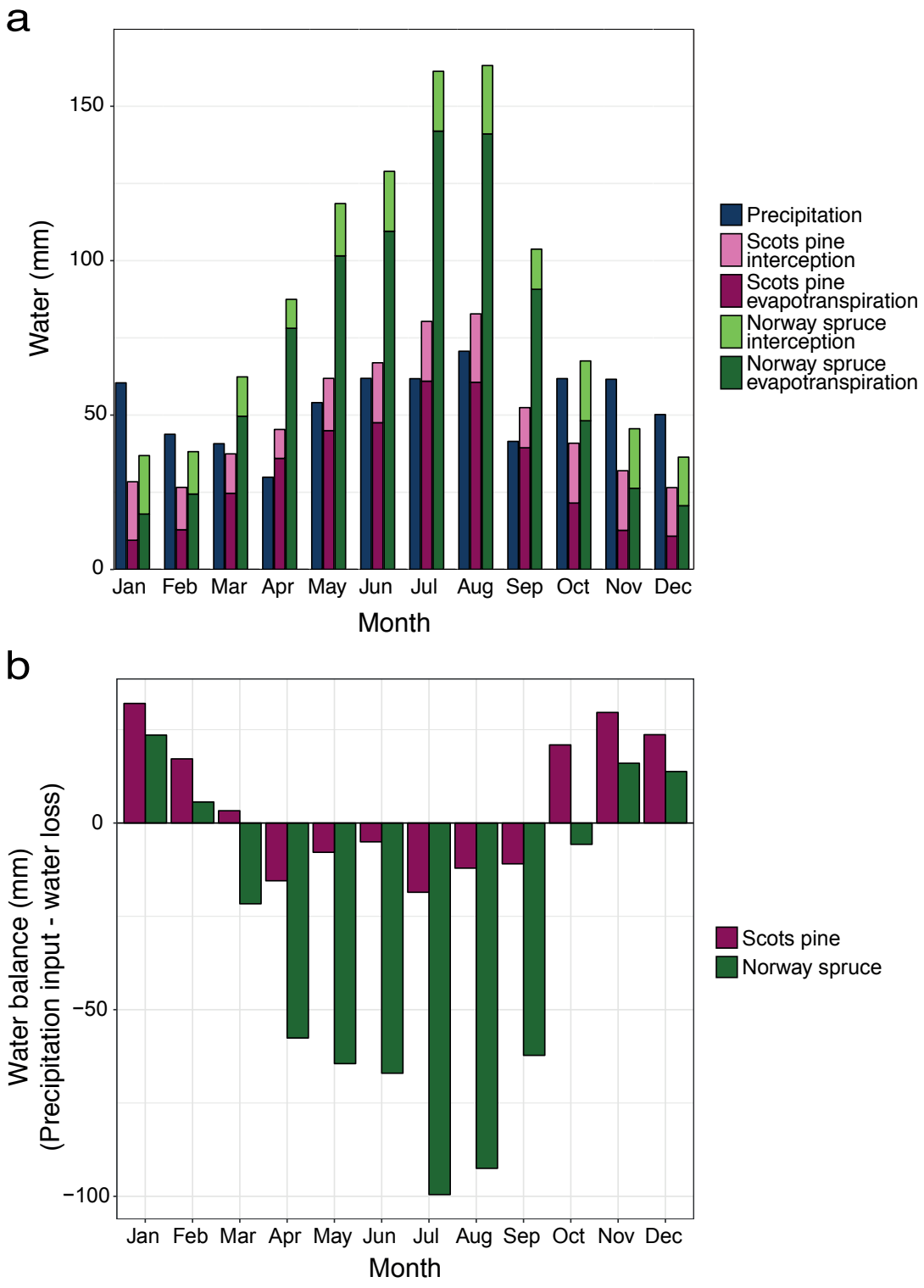

Figure 5.3: Monthly water balance for Scots pine and Norway spruce. a) Precipitation and potential evapotranspiration rates of each species. b) Total water balance (precipitation – [interception + evapotranspiration]) for each species.

Checking estimates

Gash & Stewart (1977) estimated total transpiration from a Scots pine stand in Thetford Forest in 1975 to be 352.8 mm, using a correction factor to account for canopy wetting; without a correction factor estimated transpiration increased to 367.8 mm [215]. Using weather data from 1975, I calculated annual potential evapotranspiration of Scots pine to be 404.3 mm. Figure 5.4 shows that the cumulative (uncorrected) transpiration values of Gash & Stewart (black line) track my predictions (blue line) closely, with larger deviations only apparent towards the end of the year. There was no significant difference between datasets (P = 0.91). The current predictions for potential evapotranspiration from Scots pine (Figure 5.4, green line) were consistently higher than in 1975. By the end of the year, cumulative potential evapotranspiration is more than 50 mm higher than in 1975, which is largely as a result of an overall increase in the maximum and minimum monthly temperatures (of around 0.6°C).

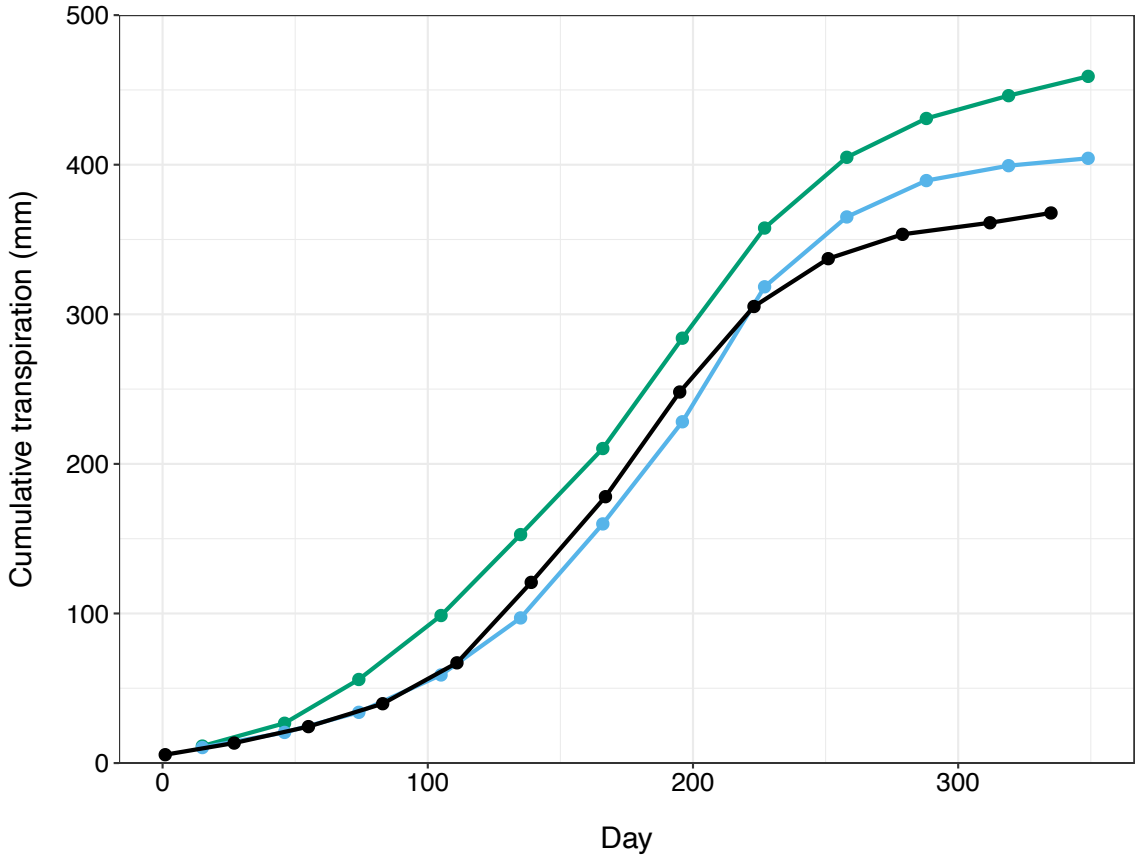

*Figure 5.4: Cumulative transpiration values for Scots pine in Thetford Forest. The black indicates the (uncorrected, i.e. transpiration + 0.07*interception) cumulative values from Gash & Stewart (1975); the blue line indicates my predictions of potential evapotranspiration for 1975; the green line indicates my predictions of potential evapotranspiration for the current day.*

Using my full water loss model (equation 4), and the 1975 weather data from the UKCP09 Met Office gridded dataset, I calculated a total water loss rate from the catchment of 509.3 mm (interception: 170.86 mm, transpiration: 338.46 mm). Calculating the interception component using the precipitation data reported by Gash & Stewart (1977) [215] gave a value of 186.5 mm. This matches very closely with the total interception value reported by Gash & Stewart of the Scots pine stand (213.6 mm) minus the estimated bracken interception (27.0 mm), giving 186.6 mm.

Total volume

Managing the entire forest as conifer results in an annual potential deficit of 13.1 million m^3 water (Figure 5.5b). In contrast, managing the forest as broadleaved results in an annual recharge of at least 5.5 million m^3, whereas heathland is the best option for water balance, giving a recharge of at least 63.1 million m^3 (Figure 5.5b).

Water loss in different locations

For all scenarios, potential evapotranspiration was highest in Thetford, followed by the Forest of Dean and then Kielder; the reverse was true for interception (Kielder > Dean > Thetford), which follows annual rainfall patterns (Figure 5.6). For the heath and broadleaved scenarios, the total potential water loss followed the pattern of evapotranspiration: Thetford > Dean > Kielder (Figure 5.6). However, for conifers, the high interception losses from the Dean was sufficient to compensate for the high potential evapotranspiration losses in Thetford, so order of greatest potential water loss was Dean > Thetford > Kielder (Figure 5.6).

In Thetford, the relatively low annual rainfall means that total potential water loss from conifers exceeded precipitation input (Figure 5.5 and Figure 5.6). However, in Kielder and the Dean, the annual rainfall comfortably exceeds the total potential water loss from all the different scenarios (Figure 5.6).

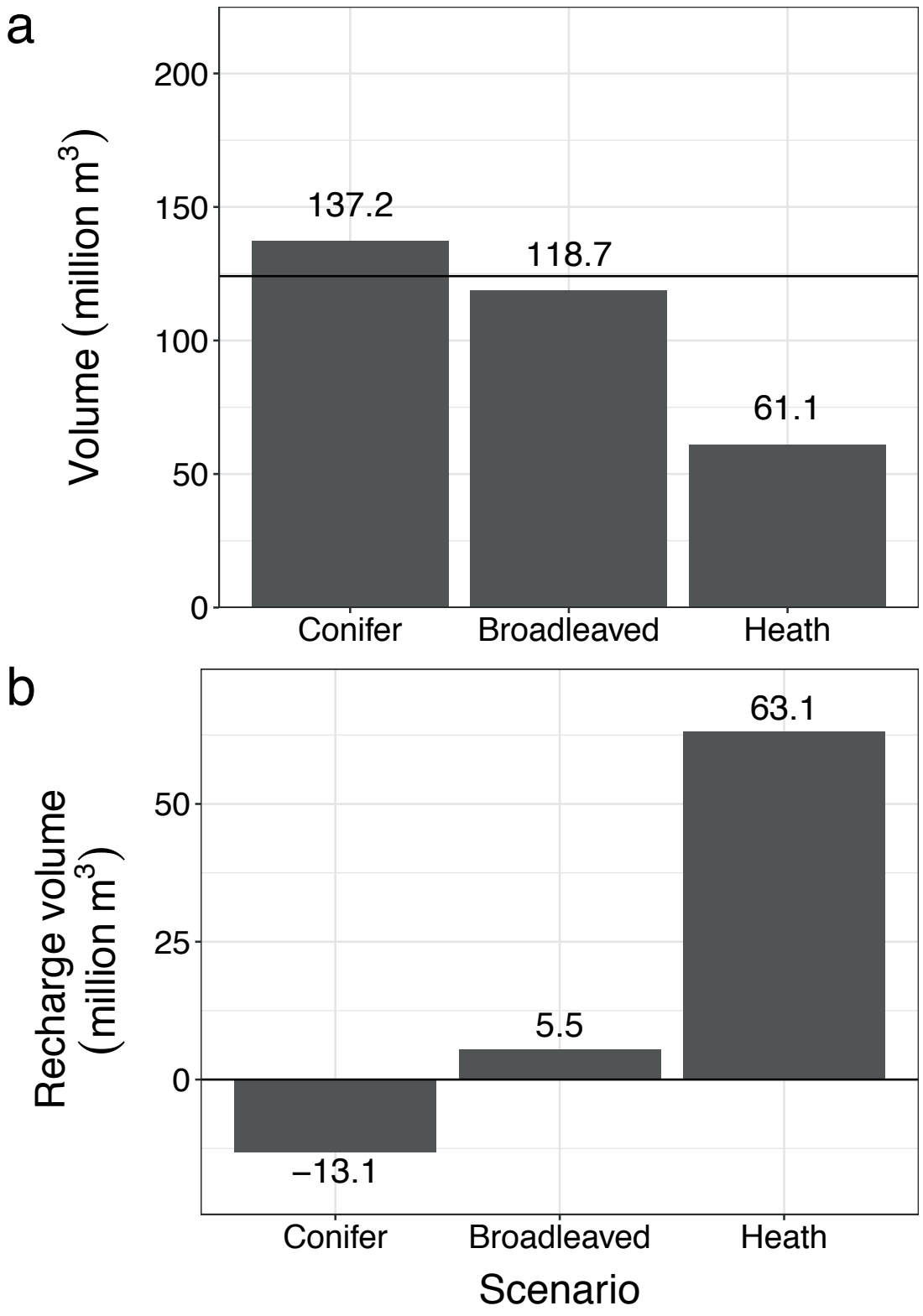

Figure 5.5: (a) Total potential volume (across the forest) of water lost for each scenario in a year. Horizontal line indicates annual rainfall input (124.1 million m^3) (b) Total water balance (rainfall input – total potential water loss) of forest for each scenario.

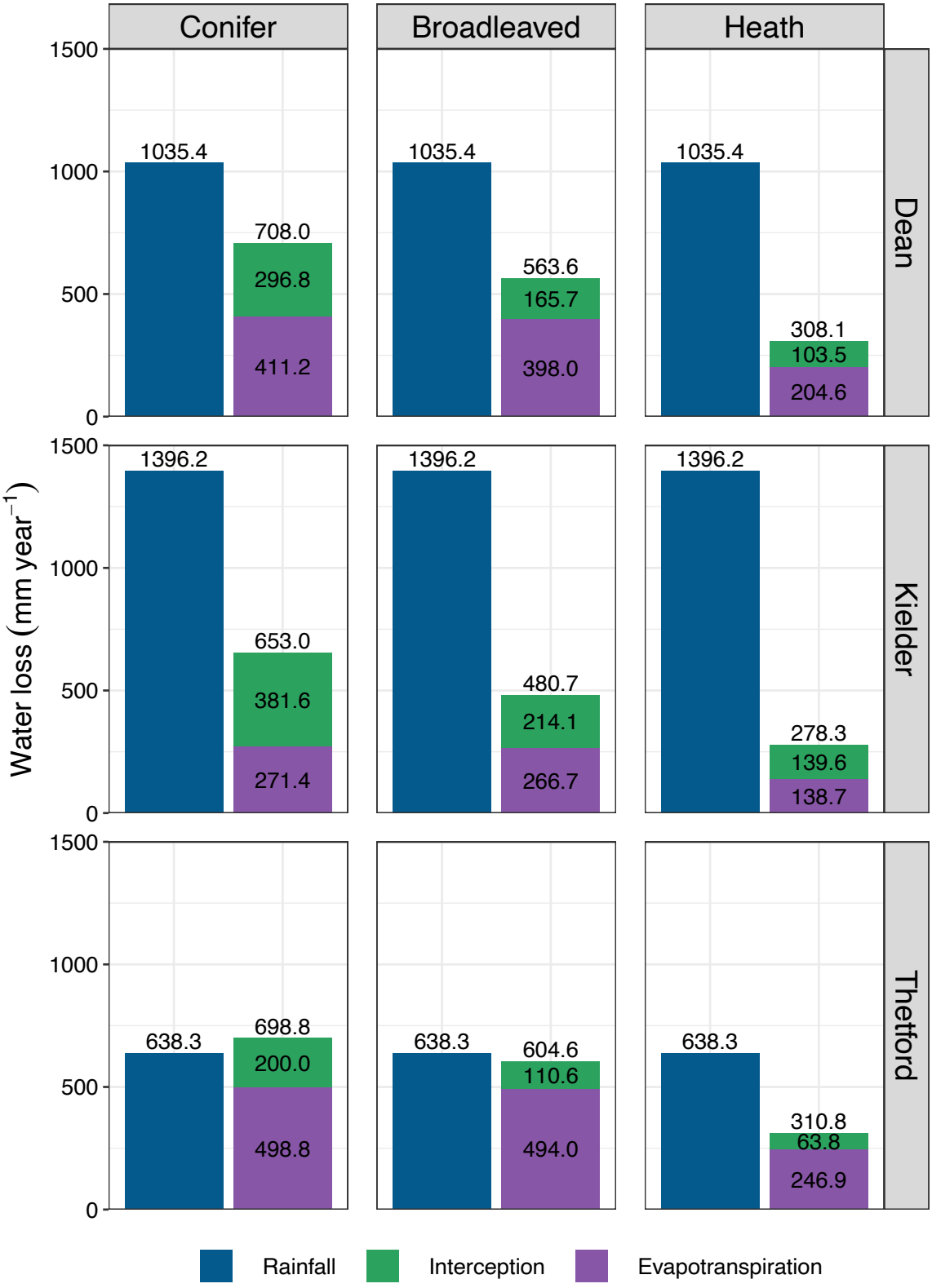

Figure 5.6: Total potential water loss of different scenarios, alongside annual average rainfall, in different UK forestry locations.

Effects of climatic variables on water loss

Rainfall

As rainfall input increases, potential evapotranspiration slightly decreases (as it only occurs when the canopy is dry, and increased rainfall input increases canopy wetness time) but interception loss increases (in proportion to total rainfall) (Figure 5.7a). The increase in interception loss is much greater than the decrease in potential evapotranspiration rate, so total water loss increases with increasing rainfall input (Figure 5.7a). However, total potential water loss does not increase as quickly as total rainfall, so the overall ratio of potential water loss to precipitation decreases (Figure 5.7b). For the Thetford Forest region, an average addition of 10 mm of rainfall a month would be sufficient for the annual rainfall input to be greater than the annual total potential water loss from conifers (Figure 5.7b).

Other climatic variables

Maximum temperature and vapour pressure had large effects on the potential evapotranspiration rate, as, to a lesser extent, did minimum temperature (Figure 5.8). Increasing minimum and maximum temperature increased the potential evapotranspiration rate; however, mean temperature did not have a great effect on potential evapotranspiration rate (Figure 5.8). Increasing vapour pressure reduced potential evapotranspiration rate. Hours of sunshine and elevation had negligible effects on potential evapotranspiration rate (Figure 5.8).

The relatively large negative differences in maximum and minimum temperature between Kielder and Thetford explain the lower evapotranspiration rate in Kielder (despite the compensatory effect of a lower vapour pressure) (Figure 5.6 and Figure 5.8). This pattern is mirrored, to a lesser extent, between the Forest of Dean and Thetford (Figure 5.6 and Figure 5.8).

In the Thetford Forest region, the potential evapotranspiration estimates for Scots pine for different 5km squares ranged from 418.8 mm to 484.5 mm per year (mean: 448.8 mm, standard deviation: 15.8 mm). As demonstrated in Figure 5.9, altering the maximum and minimum temperatures explains most of the differences in potential evapotranspiration rates. The difference between the maximum and minimum 5km squares in mean maximum and minimum monthly temperature was 0.58°C and 0.65°C respectively.

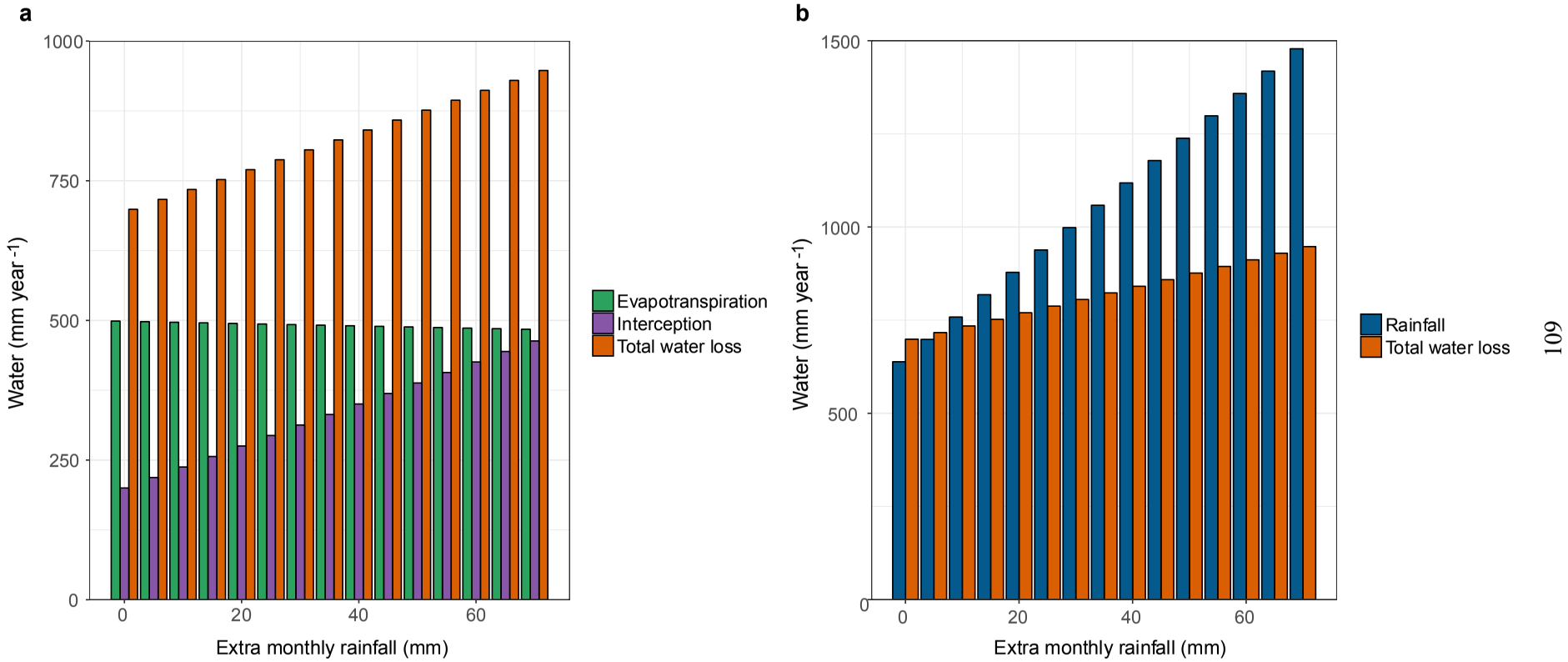

Figure 5.7: The effects of increased rainfall to the Thetford Forest system on potential water loss from conifers. (a) Total water loss is shown alongside its two components: potential evapotranspiration and interception. (b) Total water loss is shown alongside total rainfall.

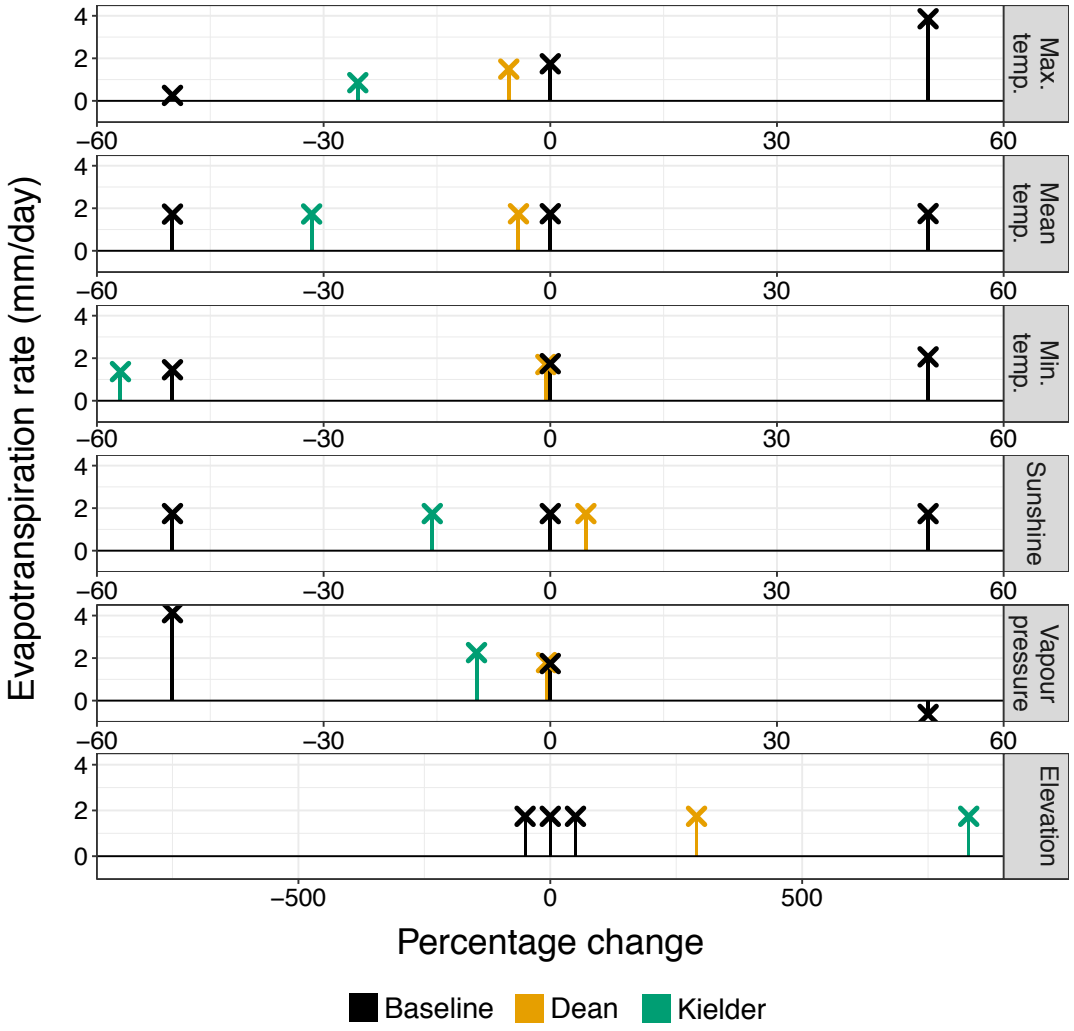

Figure 5.8: Potential evapotranspiration rate of conifers for different levels of climatic variable. To calculate evapotranspiration rates all climatic variables are kept constant at the Thetford Forest baseline except for the variable indicated. Percentage change is the magnitude of change of each climatic variable from the Thetford Forest baseline. The black points indicate the baseline of Thetford Forest (0 percentage change) and values that are 50% more or less than current Thetford values. Points for Dean and Kielder are shown at the percentage change corresponding to the magnitude of change from the Thetford Forest value. Note the change of scale of the x-axis for elevation in relation to other climatic variables.

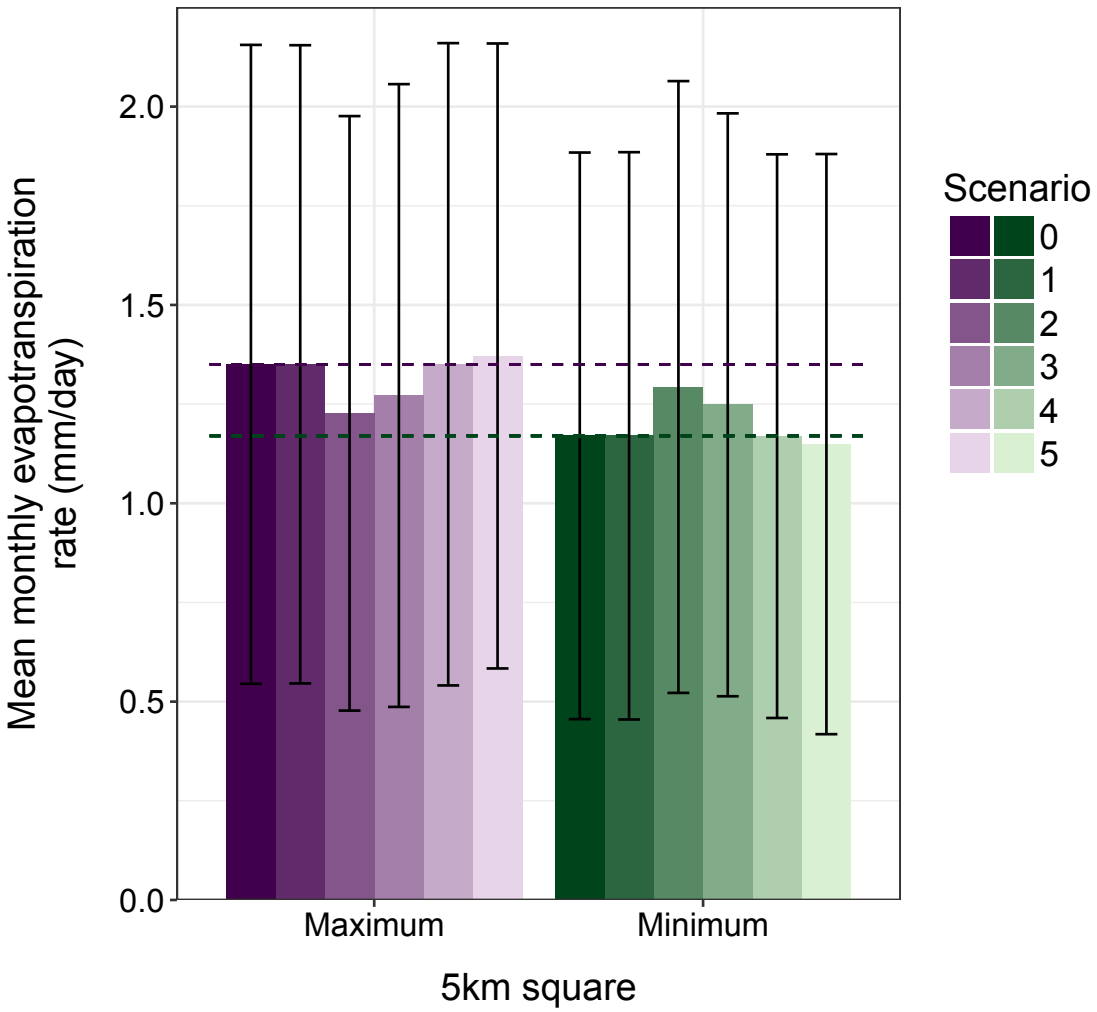

Figure 5.9: The values of the mean monthly potential evapotranspiration rate for each of the scenarios in Table 5.3, using either the maximum or minimum 5km square weather variables as default. The horizontal lines indicate the values of the no change scenario (scenario 0). Error bars are standard deviation across the months.

Climate change predictions

Under a low emissions scenario with climate predictions for the 2080s, potential total water loss from a Scots pine management scenario was predicted to be 611.8 mm per year (interception: 189.7 mm; potential evapotranspiration: 422.1 mm). Total potential water loss is therefore predicted to be slightly higher than current levels; interception will decrease (due to lower overall precipitation levels) but these models predict an increase in potential evapotranspiration.

However, over the winter months, the remaining precipitation that is not intercepted exceeds potential evapotranspiration rates (Figure 5.10). In contrast, between April to September, potential evapotranspiration is greater than remaining precipitation (after interception) (Figure 5.10). The

potential evapotranspiration rates are 1.7 times greater than the remaining precipitation after interception in July and August. Over the whole year, the total water balance is -6.55 mm.

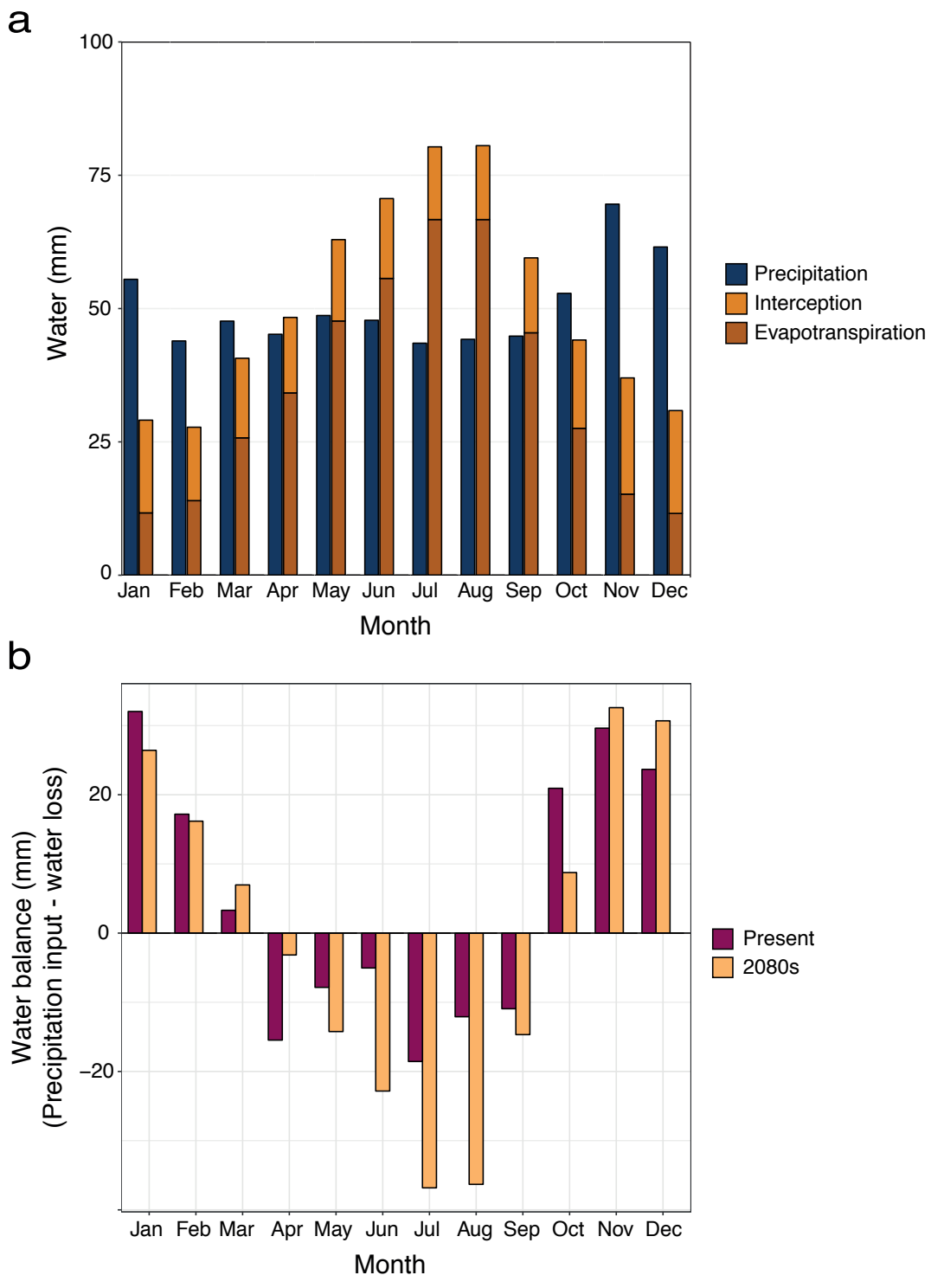

Figure 5.10: Monthly water balance for Scots pine, predicted for 2080s, using UKCP09 low emissions predictions. a) Precipitation, interception and potential evapotranspiration rates. b) Total water balance (precipitation – [interception + evapotranspiration]). Values from climate change predictions are shown alongside predictions from present-day (Figure 5.3).

DISCUSSION

In Thetford Forest, my models predict that conifers contribute the greatest potential water loss, at a rate of 698.8 mm/year (Figure 5.2). This exceeds the average annual precipitation input (638.3 mm), resulting in a potential water deficit of 13.1 million m^3 (Figure 5.5). In contrast, the potential water loss from broadleaves (604.6 mm/year) is below the annual precipitation threshold, and heath is much lower (310.8 mm/year). The heath estimate is lower than might be expected, which probably reflects the difficulty in estimating an accurate surface resistance (due to limited leaf area index measurements of rough grassland species). However, both broadleaves and heath are better options than conifers for overall water supply.

Importantly, there is seasonal variation in the water balance patterns, with my calculations predicting that rainfall input exceeds interception and potential evapotranspiration rates over the winter months, and potential evapotranspiration of conifers exceeds precipitation in the summer months (Figure 5.3). The soils under Thetford Forest are highly variable, being a mosaic of deep sand drifts and shallow sand over chalk [57], and the overall impact on trees of this seasonal variation in water balance will depend on the underlying soil type. Whereas sandy soils are freely draining, with little water available to vegetation, on chalk it is possible for trees to maintain water supply through capillary action to the roots [204,233]. Therefore, while there may be aquifer recharge over the winter months when precipitation input exceeds interception and potential evapotranspiration, the extent to which vegetation can access this water, and the resultant water stress, in the summer months is dependent on the depth to chalk. In sandy areas where tree roots are unable to reach the chalk, trees will reduce their transpiration rates by closing their stomata in times of water stress over the summer months [204,234]. This will inhibit tree growth due to lack of CO_2 assimilation, with implications for forestry management, but will not result in a water deficit as potential evapotranspiration rates will not be reached. In contrast, on soils where tree roots can reach the chalk, there is potential for trees to reach higher evapotranspiration rates than precipitation input in the summer months. This may then lead to an overall water supply deficit, especially in areas of high aquifer transmissivity (horizontal movement of water).

These imbalances are likely to be exacerbated with climate change. In particular, although there is predicted to be generally higher evapotranspiration rates in the 2080s, according to my calculations this is outweighed by the increase in precipitation in November and December, so there is potential for slightly more recharge in these months than presently (Figure 5.10). However, I predict much greater water stress over the summer months, and potentially a greater water deficit if trees can access groundwater, due to less precipitation and warmer temperatures (Figure 5.10). Indeed, the estimates for total annual water balance for Scots pine shifts from currently being below rainfall input by 56.8 mm, to being greater than rainfall input by 6.55 mm in the 2080s. However, these

models do not take into account changing CO_2 levels, which may have a variety of effects on tree productivity and water use. Elevated atmospheric CO_2 concentrations can lead to increased biomass and leaf area index [235,236]. However, there is also evidence that rising CO_2 levels increase water use efficiency as plants are able to maintain productivity at a decreased stomatal conductance [237,238]. Both increasing leaf area index and reduction of stomatal conductance can increase the impacts of drought, which is a likely problem in the Breckland region [239,240]. Nevertheless, there are uncertainties over how these process at the leaf-level scale translate to canopy or stand-level responses [236,241]. Coupled with the complexity of feedback loops and interactions between different processes (such as seasonal rainfall patterns), it is therefore difficult to predict exactly what the implications of climate change may be [239,242]. However, water use of vegetation will almost certainly change in future, and it seems likely that trees will experience increased water stress over summer months. This has potentially serious implications for the future viability of plantation forestry in the region.

This study has also demonstrated the importance of forest location in affecting water loss from different management scenarios. Even across the Thetford forest landscape, small differences in temperature leads to a range of 65.7 mm/year in estimates for Scots pine potential evapotranspiration rates. The potential evapotranspiration rates across all species are consistently higher in Thetford than those estimated from the Forest of Dean and Kielder (Figure 5.6), largely due to the higher minimum and maximum temperatures in Thetford (Figure 5.8). In addition, the increased precipitation input in the Forest of Dean and particularly Kielder means that, although interception loss increases, total water loss is much lower than the rainfall threshold (Figure 5.6 and Figure 5.7). In contrast, in Thetford the relationship between rainfall and water use is much more finely balanced, with greater potential for water stress and deficit (Figure 5.6). However, the importance of different water ecosystem services also differs between the regions. Flooding is an important consideration in areas such as the Forest of Dean and Kielder, whereas it is not currently an issue in Thetford due to the low rainfall and freely draining, sandy soils. Therefore, management recommendations are contrasting; planting high water-use conifers may be the best strategy to alleviate flooding in the Forest of Dean and Kielder, but the opposite is true in Thetford where water supply is the larger concern [195].

There are clearly important implications for future forest management. These results have highlighted the delicate balance in Thetford Forest between precipitation input and the water use of different scenarios or species. For example, the stark difference between Scots pine and Norway spruce, and also (although to a lesser extent) between beech and other broadleaved species (Figure 5.2). The potential water use of these different species, and the likelihood of stress in dry conditions (which will almost certainly be exacerbated with climate change), has consequences not only for timber quality but also for wider forest resilience [239]. Successful tree species selection and

establishment will require spatial considerations, as the underlying soil types are of fundamental importance. The speed with which the roots of young trees will be able to reach chalk (if ever) and therefore access a more stable water supply will determine the relative importance of species drought tolerance. In parallel to this, it will be important to consider how potential abstraction from the underlying aquifers to meet projected increased demand for public consumption or agriculture will affect the future potential for trees to access this groundwater [197,200]. Furthermore, in addition to species choice, the future management and design of forest stands in Thetford should be carefully considered. For example, increasing the proportion of continuous-cover forestry may lead to an increase in evapotranspiration from a rougher canopy and higher aerodynamic resistance, but a reduction in interception due to more uneven canopy coverage [204].

Model performance

Transpiration rates of trees in the UK (and Europe) are thought to be relatively consistent, with an expected range of around 300-400 mm/year [204,243]. Numerous reasons have been put forward for this, such as regulatory mechanisms including stomatal closure under water stress or increasing vapour pressure, and the presence or absence of an understorey [233,243,244]. For example, the understorey of forest stands are thought to be an important moderating factor: lower foliage density (with low evapotranspiration rates) is likely to lead to higher understorey density due to increased light levels, which in turn contributes evapotranspiration; in contrast, higher foliage density (with high evapotranspiration rates) will prohibit understorey development [243]. In Thetford Forest, a comparison between Corsican pine (with relatively high leaf area index and higher transpiration rates) and Scots pine (with vigorous bracken understorey) found similar total transpiration rates [245]. My potential evapotranspiration rates for Scots pine, birch and oak match the expected ranges well (Figure 5.2). However, Norway spruce, beech, and the general conifer and broadleaved scenarios have higher potential evapotranspiration rates than the general 300-400 mm/year range (Figure 5.2), due to a higher leaf area index value (Table 5.2), and the relatively warm and dry climate in Thetford Forest. This is not unexpected and has been observed previously: for example, Calder (1977) predicted transpiration losses from Norway spruce of 290-340 mm/year in Wales, but the same model run in Thetford Forest predicted much higher transpiration rates (the actual value is not reported, except that it is substantially higher than the Scots pine value of 353 mm/year) [243,246].

It is also interesting to observe the difference in model outputs between 1975 and the present day (Figure 5.4), with a consistently higher potential evapotranspiration rate in the present day (due to higher temperatures). Many formative studies of transpiration rates from trees took place several decades ago (e.g. [215,243,247]), and so the differences in climate will also partially explain higher model outputs of potential evapotranspiration rates. It is also possible that deviations from expected values may be due to using aerodynamic resistance values following Mu et al. (2011) [214], rather than

calculating aerodynamic resistance as a function of wind speed. However, Ershadi et al. (2015) [217] note that parameterising aerodynamic resistance values following the Mu model [214] is the best option when wind data collected from above the tree canopy are not available, as was the case in this study. Furthermore, the values for broadleaved and conifer aerodynamic resistances are within the range of those reported elsewhere in the literatures (e.g. Hall [1996] [248], Stewart and Thom [1973] [232]). Finally, my models perform well when compared to the previous results of a Scots pine stand in Thetford Forest [215], with no significant difference between the predictions for potential evapotranspiration. As the weather data used by Gash & Stewart (1977) [215] were not available I had to use 5km UKCP09 [207] values. Given that climatic data can have large effects on the predicted potential evapotranspiration rates (as discussed above), this may explain the deviations towards the end of the year (Figure 5.4).

Clearly, there are lots of adaptations that could be made to the models in an attempt to improve estimates of total water loss. For example, in their evaporation model of Scots pine in Thetford Forest, Gash & Stewart (1977) [215] include bracken interception, although they do not include bracken transpiration (which as measured by Roberts et al. (1980) [249] contributes around 20-25% of total transpiration). By adapting the Calder-Newson model [205], I attempt to account for the variability in canopy cover by including a non-forest and forest area term. I substitute non-forested areas to be rough grassland, as this is the vegetation that predominates in open space areas, such as rides, throughout the forest (although potentially under-estimates water loss where bracken thrives such as on acidic soils under Scots pine). Finally, surface resistance obviously has a big effect on the predicted potential evapotranspiration, and so values of stomatal resistance and leaf area index are key (as demonstrated for example by the difference between Norway spruce and Scots pine, Table 5.2). Although some of the datasets that I summarised were extensive (such as stomatal resistance for rough heathland species and leaf area index values for trees), others were less good, with resultant potential effects on the model estimates. Clearly, it would be best to have data collected in Thetford to input to the models, but in the absence of this, these results represent a best estimate. Nevertheless, it is important to remember that the values produced in this study are estimates, and model errors and uncertainty are likely to be a factor in determining the differences between species, scenarios or locations.

6 | Quantifying cultural ecosystem services: disentangling the effects of management from landscape features

SUMMARY

1. Cultural ecosystem services are undeniably important, yet are typically neglected in land management decisions due to a suite of intractable challenges: they are highly complex, localised, and inextricably associated with landscape features. However, to incorporate the ecosystem services framework into land management, decision makers need the tools to disentangle the effects of land use from other factors. This is a major challenge for ecosystem services research.
2. Forestry is a widespread land use that has considerable potential to deliver a broad range of ecosystem services, although this requires careful management planning. Additionally, modern production forestry is undergoing a period of rapid change in the face of a plethora of challenges, such as climate change and disease. To increase cultural ecosystem services delivery from forests, managers need tools to understand the implications of different management options.
3. In this paper, we directly test how land use affects cultural ecosystem services. We use a new approach that recognises the underlying complexity of cultural ecosystem services but produces easily interpretable results that are locally relevant and directly applicable to land management. By combining participatory GIS and a novel site matching technique, we relate cultural values explicitly to land management, while accounting for the influence of landscape features.
4. Applying this new method to a major UK forest site, we conducted a large survey to gather participatory GIS data points. We showed that land management significantly affected cultural ecosystem service values and were able to make a series of practical forest management recommendations. Notably, a greater diversity of tree species would improve cultural value, and open space is important within the forest landscape.
5. This approach is highly flexible and can be applied to any type of landscape. It allows cultural ecosystem services to be fully integrated into land management decisions to formulate the best management strategy to maximise ecosystem service delivery.

INTRODUCTION

People derive a range of goods and benefits from ecosystem services, which are produced by processes in the natural environment [1,13]. Ecosystem services are commonly grouped into provisioning (such as food, fibre and timber), regulating (such as climate regulation and water purification) and cultural (such as aesthetics and recreation). They are underpinned by supporting ecosystem services (such as primary production and nutrient cycling) [1]. There has been a dramatic increase in ecosystem service research over the past decade, with good progress in incorporating the results into policy and practice [19,250]. However, the majority of this research has focussed on provisioning and regulating services [30], while cultural services have been relatively neglected [20,35]. This may be because cultural ecosystem services are widely considered to be inherently difficult to quantify [251–253]: while many ecosystem services relate to easily measured biophysical processes or changes [254,255], cultural services include intangible concepts such as aesthetic value [252,256]. Furthermore, people value cultural services in different ways, and these values can change over time [257,258]. Therefore, despite recognition of their importance [252,259], cultural ecosystem services are frequently ignored or play a minimal role in valuation exercises [37].

In recent years, people are interacting less with nature. This change in behaviour has been attributed to urbanisation, biodiversity loss, technological changes and safety concerns [260,261]. However, there is a large body of evidence that demonstrates that exposure and relatedness to nature is beneficial for physical and mental health [262–264]. Additionally, poor connectedness to nature can reduce pro-environmental behaviour and drive unsustainable attitudes to resource use, and so re-connecting people with nature will have an important role to play in responding to global ecological challenges [265,266]. In this context, cultural ecosystem services – which are broadly defined as the non-material benefits from ecosystems [267] – has clear potential to help address this challenge. By quantifying how people engage with and value the natural environment, we can find ways of encouraging exposure and maximising the positive benefits.

People and the natural environment are intimately linked in the production of ecosystem services and benefits. Ecological processes generate ecosystem services but, often, people manage the environment to influence this process [13]. Equally, with the addition of other inputs, people convert flows of services into benefits and goods that are of use. Therefore, ecosystem services are 'co-produced' by both nature and people [268,269]. Furthermore, relational values – which are derived from relationships and interactions, such as between humans and nature – are now widely recognised to be an important additional perspective to more traditional intrinsic and instrumental value framings [24,270,271]. Fish, Church, and Winter [272] proposed a conceptual framework for cultural ecosystem services, which considers them in terms of cultural practices and environmental spaces. The framework links cultural ecosystem services to their geographical context (environmental spaces

enable cultural practices). It also explicitly incorporates the relational values of cultural ecosystem services, following the work of Chan et al. [267,273], which recognises that cultural values "arise from human-ecosystem relationships"; the environment both shapes and is shaped by human actions.

A common goal of ecosystem services research is to understand how we can increase the overall delivery and diversity of ecosystem services produced from different landscapes (environmental spaces). In particular, for the ecosystem services framework to translate into practical land management, decision-makers must have the tools to understand how land use affects the delivery of different ecosystem services in order to decide what to prioritise or how to achieve the best compromise [4,25,274]. For cultural ecosystem services, this is complicated by the fact that they are influenced by many factors, such as natural landscape features, heritage and history, current land management practices, and how people interact with the environment [8]. Disentangling the effects of current land management from factors that are relatively fixed (such as the location of natural features) remains a major challenge for ecosystem services research.

The investigation of cultural ecosystem services is particularly well suited to spatial analysis. A range of sociocultural phenomena influence how people value ecosystem services: preferences are the result of how an individual perceives nature's benefits, which in turn is influenced by a variety of internal and external factors (such as core values and social structures) [275]. Such preferences can be measured as cultural values that are assigned to particular environmental spaces, i.e. places [275–277]. In particular, participatory GIS is increasingly used as a method to engage stakeholders in the mapping of ecosystem services [278,279]. Often, the results from such exercises are descriptive, focussing on the spatial distribution of ecosystem services across the landscape, frequently involving the creation of density – or 'hotspot' – maps [278]. Various studies have related cultural values to land use [277,280,281]. However, the places that people visit or value are influenced by a wide range of factors in addition to land management, such as ease of access or location of visitor centres [277]. In this paper, we present a novel methodology that aims to relate spatially assigned cultural values directly to management by accounting for these other features in the environmental space.

More than half of the world's forests are production or multi-purpose forests [45], and when managed carefully and sustainably they have significant potential for the provision of a wide range of ecosystem services [12,282]. However, forestry in general is under increasing threat from various factors including disease [48,283] and climate change [50,284]. For example, Corsican pine, Japanese larch and ash, are all important species in British forestry that are currently undergoing major declines or being rendered unviable as a result of pathogen outbreaks [48]. Forest management worldwide urgently needs to be rethought to increase forest resilience [285–287]. At the same time, forest owners are increasingly motivated and influenced by cultural ecosystem services and seek ways to maximise multifunctionality [257,288]. Therefore, this is an opportune time to consider how forest management decisions affect the delivery of cultural ecosystem services.

There is a large body of literature exploring the aesthetic and recreational values of forested landscapes. For example, many studies have shown that people generally prefer naturalistic forests and larger trees [289–292]. However, deadwood is often viewed unfavourably, and the size of clear-cuts correlates negatively with recreational value [293–295]. In Finland, seasonality has also been shown to be important, with snow cover increasing the suitability of commercial forest stands for recreation [289]. Generally, people seem to prefer broadleaved to conifer forests, and mixtures to monocultures [12,296–300]. However, results are variable and seem to be highly context-specific; familiarity appears to be important, as do factors such as openness [291,295,299,301]. In a pan-European study of the effects of forest structural attributes on recreational values, Edwards et al. [295] found general consensus regarding the importance of many attributes, but also identified key regional differences in preferences. For example, left-over residues from forest management operations or the structural diversity of forest stands had differential importance across Europe, attributed to potentially complex people-place relationships [295], mirroring concepts proposed for cultural ecosystem services [271,302].

Although it is helpful to identify broad patterns in public perceptions towards forest attributes, particularly for the development of policy, existing research has repeatedly shown the importance of local contexts. Currently, to tailor management decisions regionally, forest managers largely use feedback on forest plans, conversations with visitors, or complaints, as their basis for identifying the types of forestry land management that visitors prefer. Additionally, most studies to date have focused on broad preferences, rather than specific cultural ecosystem services, and there is an overall bias towards recreation and aesthetic cultural values [292,300]. Similarly, much research has been based on hypothetical scenarios and uses stated preference methods (such as choice experiments) [292,303]. The potential limitations of stated preference methods are well documented, as people's behaviour and actions often differ from their statements [304]. If forest managers are to more effectively incorporate planning for ecosystem services into forest design, they need the tools to understand how real forest management alternatives are valued in their local contexts. This includes the potential trade-offs and synergies between the full range of cultural services.

In this paper, we address these research gaps using a novel quantitative methodology that relates cultural ecosystem services directly to the management of the landscape. We first use a large participatory GIS survey to map the distribution of different cultural values, then implement a site matching technique to control for the effects of landscape features. We apply our methodology to Thetford Forest – a large commercial plantation in East Anglia, England – to explore how forest management affects cultural values. We test four hypotheses. First, that cultural ecosystem service values vary with land management (hypothesis one). Then, three hypotheses based on existing literature, forest managers' impressions of visitor preferences for land management, and knowledge of the regional context. The wider East Anglian landscape is predominantly agricultural, yet

Thetford Forest is the largest lowland forest in England; it is an important regional feature and provides significant recreational amenity [65]. We therefore hypothesise that visitors prefer forest to open landscapes (hypothesis two). Finally, we test the general, although locally variable, findings that visitors prefer broadleaved species to conifers (hypothesis three), and prefer mixtures to monocultures (hypothesis four).

METHODS

We followed the framework proposed by Fish, Church, & Winter [272] by using environmental spaces as an indicator for cultural ecosystem services, while recognising that these spaces will in turn be shaped by cultural practices. This allows us to explore why certain environmental spaces may be more important than others for cultural ecosystem services [272].

Study site

Thetford Forest is a large commercial plantation (18,719 ha), spanning the Norfolk and Suffolk border in the Breckland region of East Anglia, England (Figure 6.1). Over 50% of the forest landscape is Corsican pine or Scots pine monoculture. The main forest block lies between and around the towns of Thetford and Brandon, with a number of smaller blocks around the periphery. It is part of the UK public forest estate, managed by the Forestry Commission. Thetford Forest is designated as a Site of Special Scientific Interest for its plant and invertebrate assemblage and breeding populations of woodlark and nightjar [62]. It is also part of the Breckland Special Protection Area and Special Area of Conservation [63,64]. It additionally provides significant recreational amenity and is largely open access [65].

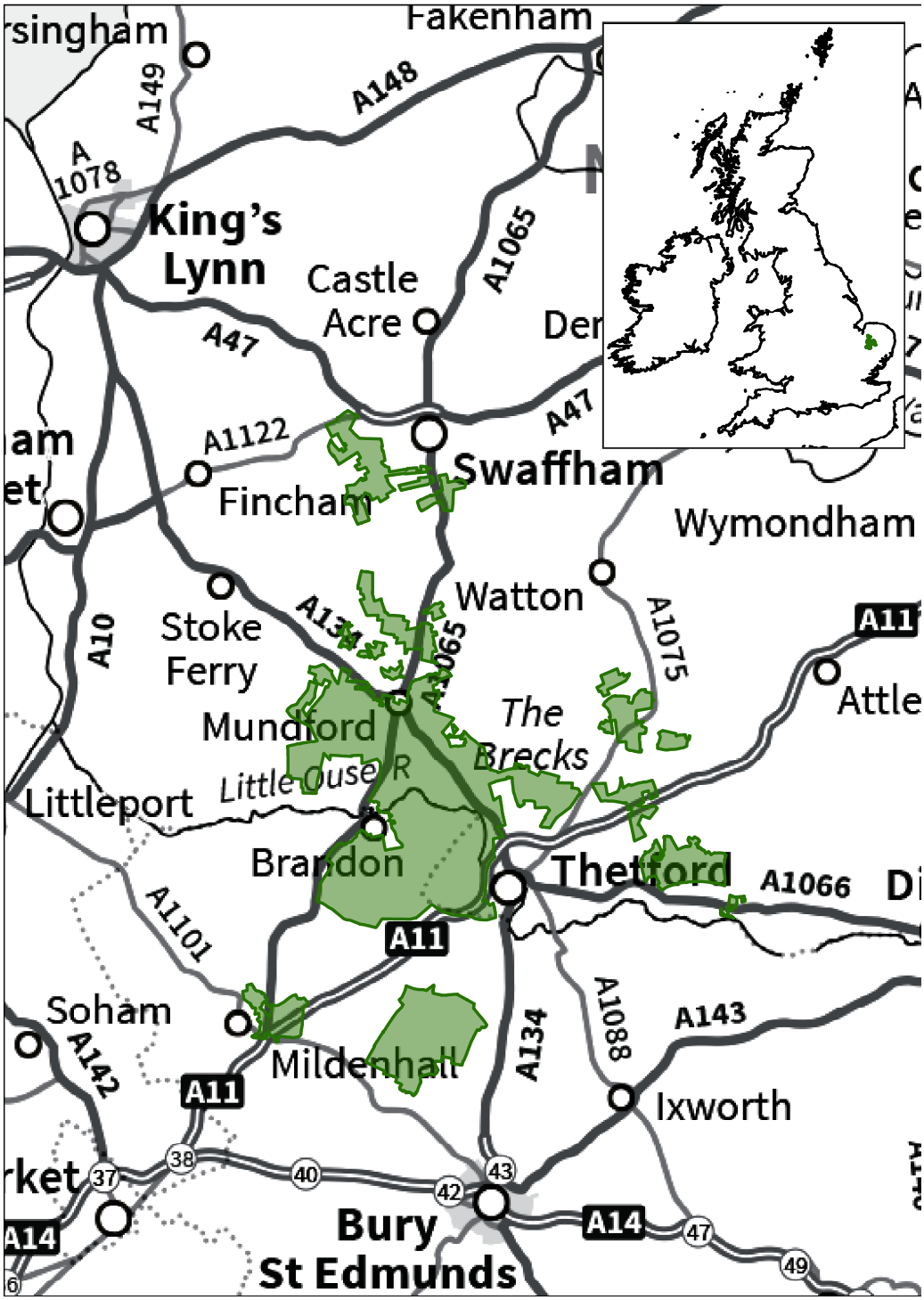

Figure 6.1: Map of Thetford Forest and surrounding region. Inset: national context map. Background map using Ordnance Survey data © Crown copyright and database right (2018).

Survey design

Cultural ecosystem services were defined by four categories: outdoors recreation, wildlife, scenic beauty and tranquillity, and heritage or educational value. These were based on commonly used categorisations of cultural ecosystem services [8,12,20,305]. To encourage participation and avoid respondent fatigue, it was important to limit the overall number of categories and corresponding survey length (in addition to creating an engaging survey experience) [306,307]. We therefore gave careful consideration to the type of landscape and existing knowledge about the key stakeholders and interests in the forest to inform our final categorisations.

An online survey was designed using participatory GIS. This technique normally involves marking points or shapes on a map [278]; however, many people struggle to communicate the value of landscapes using such constrained spatial techniques [308,309]. We therefore used the participatory GIS spraycan tool Map-Me [309], which has been designed to overcome this. The spraycan generates a series of random points within a specified radius of the computer mouse pointer for as long as the mouse button is held down. The respondents can control the location of the points by moving the mouse pointer and can indicate strength of preference by 'spraying' for longer at a specific location, which generates a higher density of points [309]. It is easy to control, logical and intuitive for the user, and offers flexibility as respondents can decide freely what patterns to mark [309]. This is especially useful in contexts such as cultural ecosystem services when questions are asked about values, which can be vague. The mapping components of the survey were prefaced by a series of optional demographic and opinion questions. These questions covered respondents' main use of the forest, familiarity with the area, perceived importance of the four cultural ecosystem services (a five-point Likert scale: very unimportant, quite unimportant, neither important nor unimportant, quite important, very important), and demography (age group, gender). Having considered the questions, the survey respondents moved on to the maps. After familiarising themselves with the spraycan technique using a test and practice map, which included full instructions for how to use the spraycan tool and a description of the key features, respondents were asked to mark separate maps with the areas of the landscape that they valued for each ecosystem service. Respondents were able to easily reset each map (erasing the data points and starting again) if they made a mistake or if they were unhappy with the location of points. They could do this multiple times until they were happy that the points they had sprayed accurately reflected their viewpoint. Each map carried a brief definition of the ecosystem service, as detailed in Table 6.1. The definitions were carefully considered to ensure that respondents could interpret them widely in line with their personal experiences; for example, heritage or educational value could encompass traditional land management practices such as extensive grazing on heathland.

Table 6.1: Definitions of each of the four ecosystem services.

Ecosystem service	Definition
Outdoors recreation	Includes any activity that you undertake in the forest for pleasure or exercise.
Wildlife	Includes all aspects of nature, such as plants, animals or natural history in general.
Heritage or educational value	Encompasses local history, archaeology, opportunities for learning about the environment, or a sense of place and belonging in the landscape and time.
Scenic beauty and tranquillity	Includes landscapes that you think are attractive, or places where you might go for peace and quiet.

The study was granted ethical approval by the University of Cambridge Psychology Research Ethics Committee (PRE.2016.058). Respondents were fully aware of the consent procedures, and their participation confirmed consent.

Survey distribution

A detailed outreach plan was formulated in partnership with the Forestry Commission to identify stakeholders and methods of reaching them. We categorised target audiences who use or have an interest in the forest. For example, these included local residents, people with specialist interests or hobbies (such as natural history, walking, mountain biking), forest visitors, and people who work in the forest (for further details see Appendix table E.1). We identified relevant organisations or groups for each target audience and contacted them directly via email to ask them to circulate information about the survey to their members or interested individuals and to invite their participation. We also circulated information on social media accounts and distributed posters and flyers around main car parks and noticeboards inviting participation. The survey ran online for six months from August 2016 to February 2017.

Analysis of survey results

Point weightings

In total, 1,037,447 points were sprayed on the four ecosystem service maps by 172 respondents. One of the great advantages of the Map-Me spraycan tool is the ease with which survey respondents can generate a high number of points intuitively, quickly and efficiently. The spraycan generates points continually as the computer mouse is held down, reflecting strength of preference for different areas. Points sprayed outside the forest boundary were excluded, as detailed management information was only available for the forest itself. The forest boundary outline was clearly marked on the map and respondents were made aware that points outside the boundary would be discounted from the analysis. We were able to identify a small number of duplicate answers (where the same

person had completed part or all of the demographic questions more than once) and retained only the most recent version. If a respondent had sprayed 30 points or fewer on a map, these were removed from the analysis (a single click of the mouse gives an average of 4.18 ± 1.21 points (mean ± standard deviation, n = 50)) as visual inspection of these points suggested that they were mistakes. After removing these individuals and duplicates, we were left with a total of 168 respondents and 984,149 points. We visually inspected the spray pattern for each respondent and ecosystem service map to ensure that there were no obviously anomalous results (e.g. words or pictures drawn). The number of points sprayed varied between respondents. Across all ecosystem service maps, each respondent sprayed an average of 2389 points (standard deviation = 6465). We weighted points to make different respondents comparable such that point weights for each respondent summed to 100 for each map. For example, if a respondent had sprayed 5000 points, each point was weighted to be 0.02, so the total was 100. We then further weighted the points according to the respondent's preference for each ecosystem service ranked on the Likert scale and given in their answers to general questions in the first part of the survey. Points were multiplied by a number from one to five (one if the respondent thought that the service was very unimportant, five if very important). Where an answer to this question was not given, they were treated as neutral, which had a weighting multiple of three. This secondary weighting prioritised areas where respondents deemed a service as important rather than unimportant.

For illustrative purposes of the weighted point distributions we generated heat maps using quartic (biweight) kernel density functions.

Matching

As the layout of the forest was not designed as an experiment, it was necessary to use matching techniques to account for the effects of covariates (Table 6.2) [310]. For example, an open space area close to a car park might be marked on the maps as highly preferred, but this is likely to be at least partly due to the proximity of the car park itself and ease of access, rather than just the open space management. Site matching is commonly used to account for this situation in ecological studies [311,312]. It is based on the principle of comparing apples to apples, rather than apples to pears. In our example, to determine whether open space is preferred to a conifer monoculture, we would want to compare the open site to a conifer monoculture site that was equally close to the car park, rather than to one that was a long way from the car park. In doing so, we attempt to account for the effect of the distance from the car park, to determine whether there is a difference between open and conifer monoculture management. Given that there are many such covariates in natural landscapes, site matching works by balancing the distribution of covariates between treatment and control groups as far as possible [310]. However, to our knowledge, it has never been applied either to cultural ecosystem services or when using participatory GIS. Additionally, the matching techniques

developed to date divide data into a treatment and a control group [313], which is inappropriate for a comparison between multiple land management treatments.

In developing this method to account for covariates, we took inspiration from coarsened exact matching [313]. Coarsened exact matching sets boundaries for the maximum imbalance tolerated for each covariate; this is particularly advantageous where there are large numbers of covariates as it removes the possibility of the imbalance on certain covariates being compromised in order to minimise overall imbalance (such as in distance matching) [314]. Through discussion with Forestry Commission staff, we identified 21 features (covariates) that could potentially influence the reasons a respondent valued or visited an area; these included features such as rivers, roads, heritage features and recreation routes. For each of these covariates, we divided the Thetford Forest landscape into different regions according to distance classes from the feature (or categorical classes if appropriate, such as soil type; Table 6.2). See Appendix table E.2 for full details. For example, Figure 6.2a shows a section of the Thetford Forest landscape divided into regions according to distance from a main river and a heritage feature. Areas of the same colour/shading in Figure 6.2a are comparable to each other across the forest landscape, because they fall into the same distance class for that covariate.

We then overlaid these regions for each covariate (Figure 6.2b) and overlaid again with the Forestry Commission subcompartment database of the forest (Figure 6.2c), which contains detailed information about the land management option, tree species composition and planting date. Internal areas not owned by the Forestry Commission (and therefore not always freely accessible to visitors) were classified as non-Forestry Commission land. This resulted in a total of 76,158 compartments across the forest landscape (Figure 6.2d).

Compartments were classified by their current land management option (Table 6.2). We conducted analysis in two tiers of land management: the first tier gave an overview of the twelve main land management options, such as conifer monoculture, broadleaved mixture, and open space. The second tier added finer detail allowing individual options to be analysed in more detail, such as Douglas fir monoculture within conifer monoculture. There are various land management types that only cover a small area of the forest, so we set a limit of a minimum of 25 compartments in the forest and at least 7.5 ha of that option across the landscape in order for a land management option to be defined as its own category. Otherwise the land management option was grouped into other options (for example, Serbian spruce monoculture was grouped into ‘other conifer’ monoculture). This was to reduce the likelihood of the production of significant results due to random variation. See Appendix table E.3 for full details of the options used in this case study. We additionally grouped all forested options (conifer monoculture, conifer mixture, broadleaved monoculture, broadleaved mixture, mixture [broadleaved and conifer]) together into one option, which allowed us to test our hypothesis that visitors prefer forest to open landscapes.

All compartments therefore were defined by their current land management and the covariate class they fit into. Different compartments across the forest could be assigned the same combination of classes for all the covariates. For example, in Figure 6.2d, all the compartments that are the same colour belong to the same classes for each covariate, but their management might differ. Overall, there were 27,878 unique combinations of the 21 covariate classes. Each unique combination (assigned a different colour in Figure 6.2d) was labelled as a different subclass; the 76,158 total compartments were then grouped by the subclass they belonged to (Table 6.2).

It is important to note that management options as defined in this paper could also be referred to as landscape features. Given that cultural ecosystem services are co-produced by the interactions between people and nature, we are not directly testing the effects of management practices, but rather the combination of management and the natural environment. In using the terminology 'covariate' and 'management option', we seek to distinguish between landscape features that are relatively fixed or static (such as rivers and roads) and landscape features that can be readily influenced through changing habitat management.

Table 6.2: Definition of terms used in methodology.

Term	Definition
Class	Boundaries used for each covariate to divide up the forest; mostly distance groups, some categorical (e.g. soil type).
Compartment	An area within the forest, assigned to a class for each covariate; also defined by their current land management.
Covariate	Landscape features that might influence reasons for visiting or valuing an area.
Management option	The type of land management for the forest compartment.
Subclass	A group of one of more compartments that have the same classes for each of the 21 covariates.

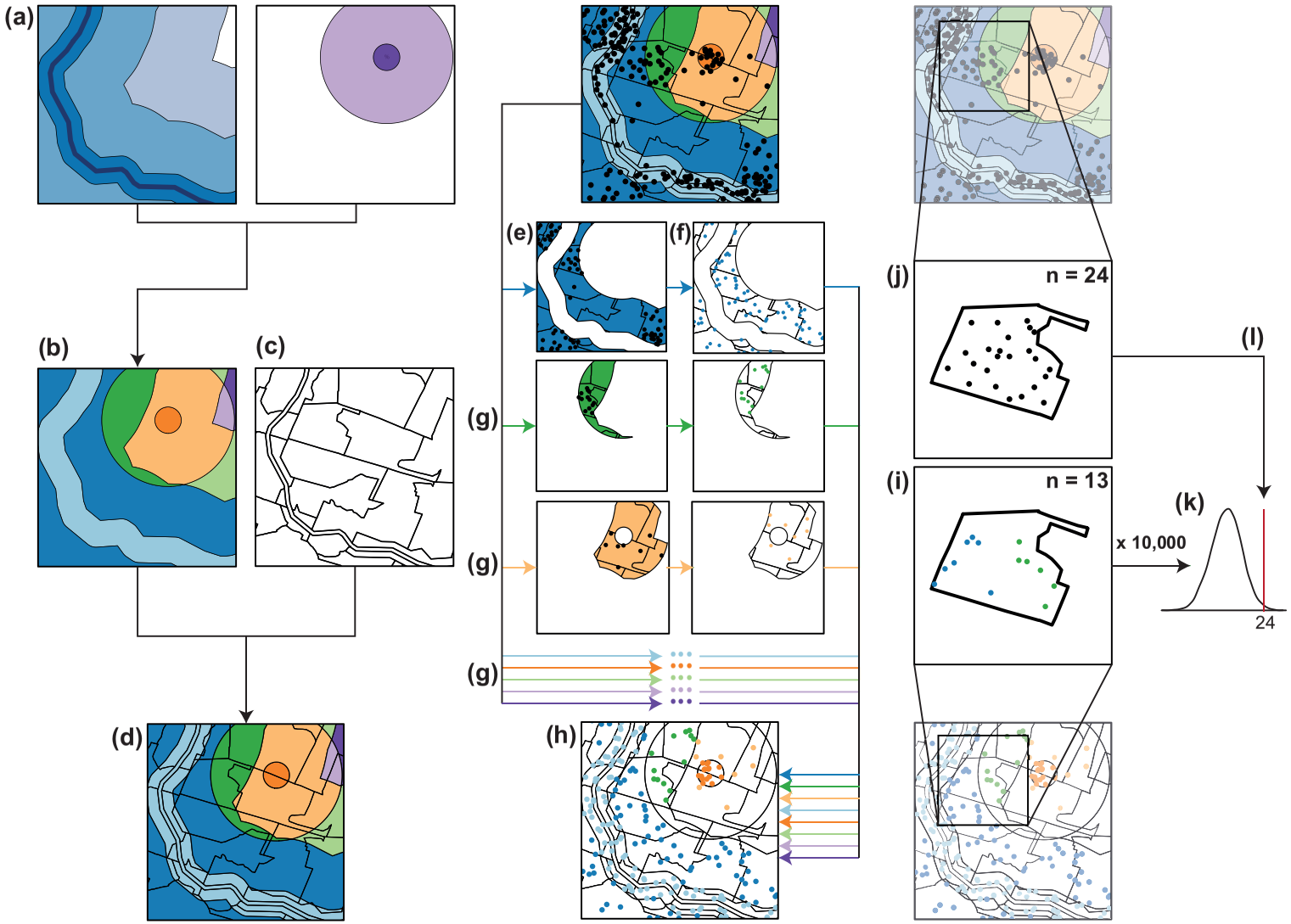
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(g)
(g)
(h)
(i)
n = 13
(j)
n = 24
(k)
x 10,000
24
(l)

Figure 6.2: Flow diagram of the methodology. a) The landscape is divided into regions according to classes for each covariate feature (left panel shows buffers for a river, right panel shows buffers for a heritage feature). b) The regions for each covariate are overlain on top of each other. The different colours represent different subclasses, which are unique combinations of classes for each covariate (for example, the dark blue regions on either side of the river belong to the same subclass because they are in the same covariate classes). c) A management database of the landscape specifies the management options for the land cover. d) The management database is overlain on top of the covariate subclasses, resulting in individual compartments that can be defined by their subclass (the class they belong to for every covariate) and their management option. e) A subclass is selected from the landscape, and the number of empirical points counted. f) The same number of points are randomly distributed across the subclass area, and the same point weightings from the empirical points are randomly assigned. g) Steps (e)-(f) are repeated for every subclass in the landscape. h) The random points from every subclass are combined to form a random distribution across the entire landscape, which takes into account the different numbers of points in different areas due to the presence of a covariate feature. i) The random points are aggregated and totalled for each management option (in the figure this is shown for just one management area). j) The empirical points in the same land management option are also aggregated and totalled. k) The whole randomisation process is repeated 10,000 times to generate a null frequency distribution of values. l) The total number of empirical points is compared to the null distribution to see if it is higher or lower than random.

Simulations

To test our hypotheses that cultural ecosystem service values vary with land management, and that respondents show preferences for different land management options, for each ecosystem service, we generated 10,000 simulations of random spray patterns of 'preferred points' as a null comparison to the empirical data. To account for matching, we generated the random points separately for each subclass of compartments. This meant that areas that received higher numbers of respondents due to, for example, being close to a car park were treated separately from areas with low respondent numbers. Points were generated using the following steps:

1. A subclass, *x*, was selected (Figure 6.2e).
2. The number of points from the empirical data across all the compartments in subclass *x* was defined as *y*.
3. The probability of a point being allocated to each compartment was in proportion to the area of the compartment (as a function of the total area in subclass *x*).
4. *y* points were randomly distributed across all compartments in subclass *x*, according to each compartment's probability (Figure 6.2f).
5. The weightings from the empirical data points were attached randomly to these simulated points.
6. Steps 4-5 were repeated 10,000 times to generate 10,000 point simulations for subclass *x*.
7. Steps 1-6 were repeated for each of the 27,878 subclasses (Figure 6.2g).
8. One of the 10,000 simulations from every subclass (selected in the order in which they were generated) was combined to form a null point distribution for the entire forest (when re-attached to one another the compartments from each subclass cover the whole forest; Figure 6.2h). This resulted in 10,000 separate point simulations for the forest landscape.
9. For each simulation, we aggregated the weighted points by land management option across the forest (Figure 6.2i).

Statistics

The empirical data were also aggregated by land management option across the forest (Figure 6.2j). Each of the sets of 10,000 simulations generated a separate null distribution of values for each management option (Figure 6.2k), which were compared to the empirical data (Figure 6.2l). *P* values were calculated as the proportion of random simulated values that were lower than or equal to the empirical value [315].

As there were multiple comparisons for each of the different sets of simulations, a Benjamini-Hochberg correction [141,142] was applied to find an appropriate level of significance for the *P* value (Table 6.3). There were 23 comparisons in total (12 broad management options: Figure 6.4, 1 forested/open: Figure 6.5 [the open plots in Figure 6.5 are a repeat of the open plots from Figure

6.4] and 10 finer management options: Figure 6.6). We used a conservative false discovery rate of 5%. All tests were two-tailed. Where P_e is the empirical data value and P_α is the Benjamini-Hochberg corrected P value, if $P_e \leq (P_\alpha/2)$ the empirical value was significantly lower than random, whereas if $P_e \geq (1 - P_\alpha/2)$ the empirical value was significantly higher than random. This allowed us to test whether any land management was valued significantly more or less than expected from random and also to distinguish between different land management options. When the P value was 0 or 1, we reported this in the text as $P < 0.0001$ or $P > 0.9999$ (as there were 10,000 simulations), and in figures as 0 or 1, respectively.

All data analysis was performed using R [143], ESRI ArcGIS 10.4 software [316] and QGIS software [317].

Table 6.3: Benjamini-Hochberg adjusted P values.

Ecosystem service	Adjusted P value (p_α)
Outdoors recreation	0.0074
Wildlife	0.0292
Heritage or educational value	0.0285
Scenic beauty and tranquillity	0.0078

RESULTS

In total, 431 people submitted usable responses to the survey, of which 168 completed map components. The number of responses differed between each of the four ecosystem service maps; outdoors recreation had the highest number of respondents whereas heritage or educational value had the fewest (Table 6.4). Hereafter, we refer to outdoors recreation as 'recreation', scenic beauty and tranquillity as 'scenic', and heritage or educational value as 'heritage'.

Of the respondents who completed the mapping components of the survey, around 60% perceived recreation, wildlife and scenic to be very important in the landscape, whereas 36% thought that heritage was very important. For each ecosystem service, fewer than 6% perceived them to be quite unimportant or very important. There was an even split between male and female respondents (48% each, 4% not given) and a spread of age groups. See Appendix table E.4 for more details of survey responses.

Table 6.4. Number of respondents for each ecosystem service map

Ecosystem service map	Number of respondents
Outdoors recreation	162
Wildlife	101
Scenic beauty and tranquillity	88
Heritage or educational value	61

Heat maps

For demonstration purposes, we generated heat maps of the weighted point density distributions (Figure 6.3). As expected, for all four ecosystem services, there was extremely high point density over the main visitor centre area (point A marked on the wildlife map). For recreation, there was also high point density over the nearby car park and river area further to the north (point B). For heritage, the Grime's Graves heritage site was also a hotspot (point C).

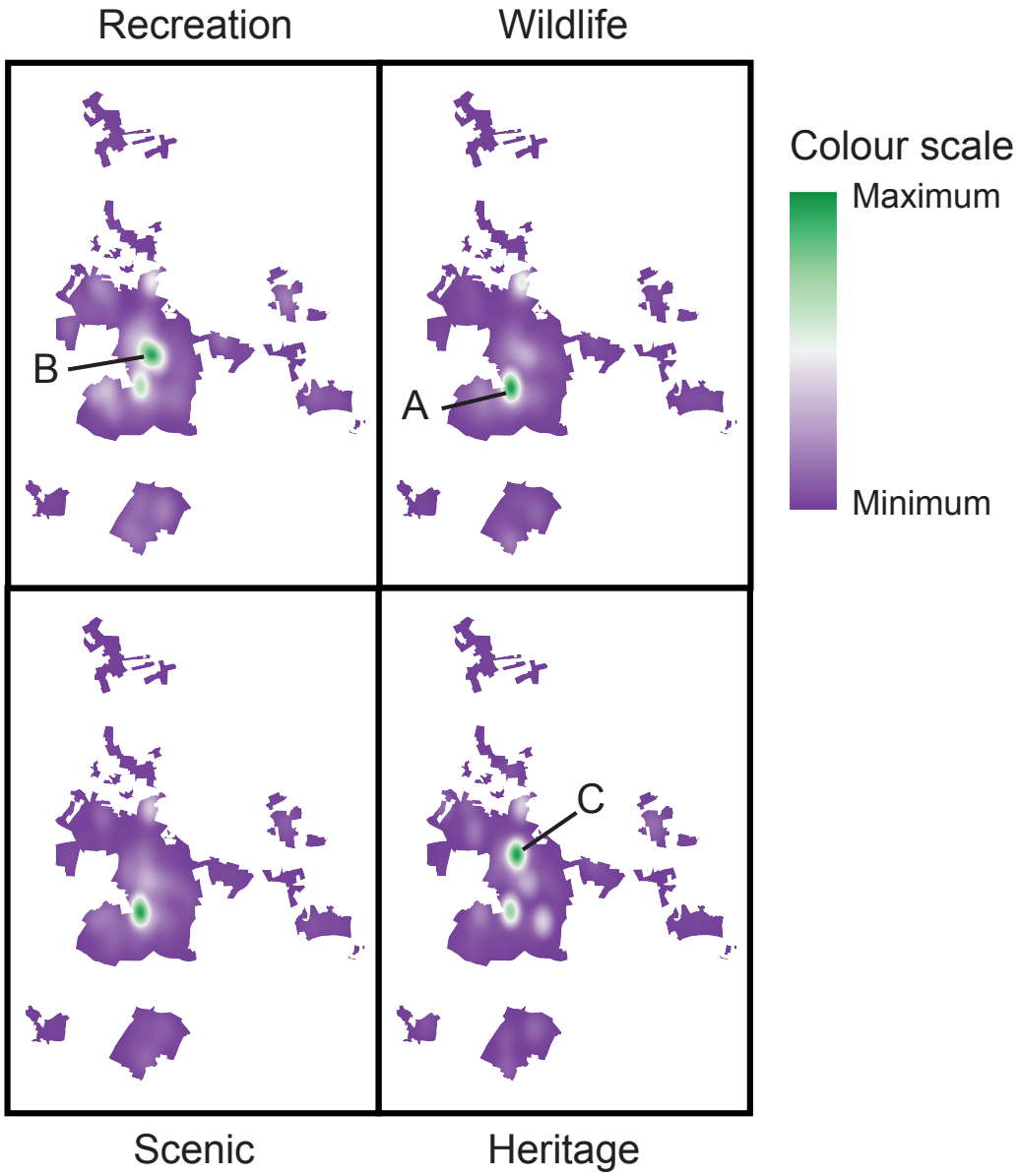

Figure 6.3: Heat maps of the weighted point density distributions for each ecosystem service. The colour scale is adjusted to show the minimum and maximum value for each map. Labelled points: (A) Visitor centre; (B) Main river and car park area; (C) Grime's Graves heritage site.

Relationship between cultural ecosystem service values and land management (hypothesis one)

We first analysed our results by dividing the landscape into 12 broad land management options (the first tier, Figure 6.4). For a third (16 out of 48) of land management options and ecosystem service combinations, land uses were valued significantly higher or lower than expected from random, even with a Benjamini-Hochberg correction factor. This confirms our first hypothesis that cultural ecosystem service values vary with land management.

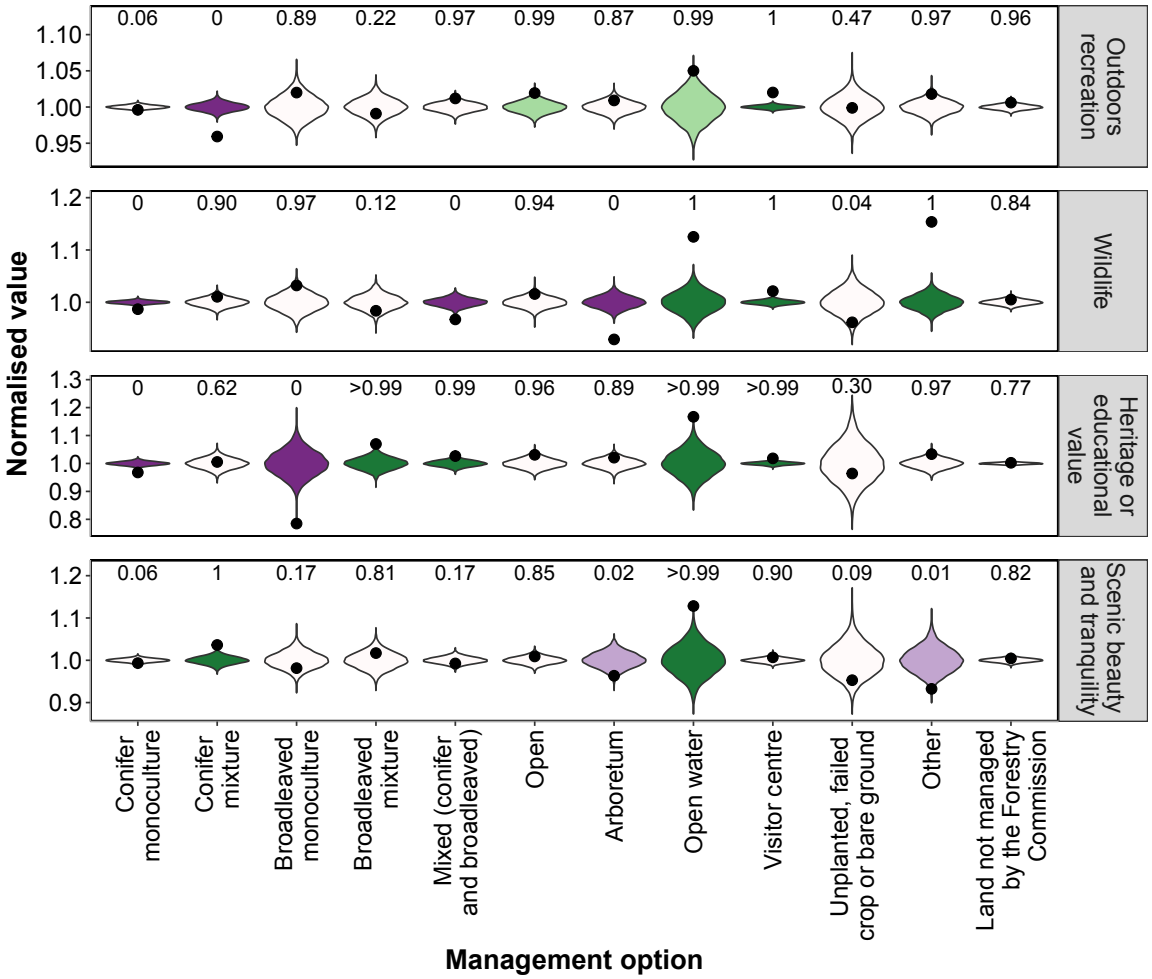

Figure 6.4: Cultural values in relation to broad management options. Values from 10,000 random simulations of point data are shown as violin plots. Empirical data values are marked in relation to the violin plots by a black point. For each management option and ecosystem service combination, all values are normalised by being plotted as a proportion of the mean of the random simulations. Violin plots are scaled to have equal width across management options. Violin plots are coloured dark green if the empirical value significantly exceeds random and dark purple if significantly lower (two-tailed); a Benjamini-Hochberg correction is calculated for each ecosystem service (see Table 6.3, methods). Plots are coloured light green or purple if the empirical values are significantly different using an unadjusted P value of 0.05 (but not with the Benjamini-Hochberg correction factor). Numbers above the plots indicate P values (the proportion of random simulations that have values lower than the value of the empirical data). Number of respondents for each ecosystem service were as follows, outdoors recreation: n = 162; wildlife: n = 101; heritage or educational value: n = 61; scenic beauty and tranquillity: n = 88.

Preferences for forests compared to open space (hypothesis two)

When all the different forested areas were combined and compared to open space (i.e. open habitat, excluding open water), the results showed that open space was valued more positively by respondents than forested areas (Figure 6.5). For recreation, wildlife and heritage, forested areas were significantly negative, indicating that respondents valued these areas less than random (all $P < 0.01$). Open space was positive for recreation, and significant when using an unadjusted P value of 0.05 ($P = 0.99$). Open space was positive, but not significant, for both wildlife and for heritage (94% and 96%, respectively, of random simulations were lower than the empirical value). Neither forested nor open space were significant for scenic. However, as shown subsequently, monocultures and conifers were viewed negatively compared to mixtures and broadleaved species, and as the majority of the forested area is monoculture (65.5%; of which 61.7% is conifer monoculture and 3.8% is broadleaved monoculture), the current composition of Thetford Forest may be negatively skewing perceptions of forest in relation to open space. These results lead us to reject our second hypothesis that forested areas are preferred to open space.

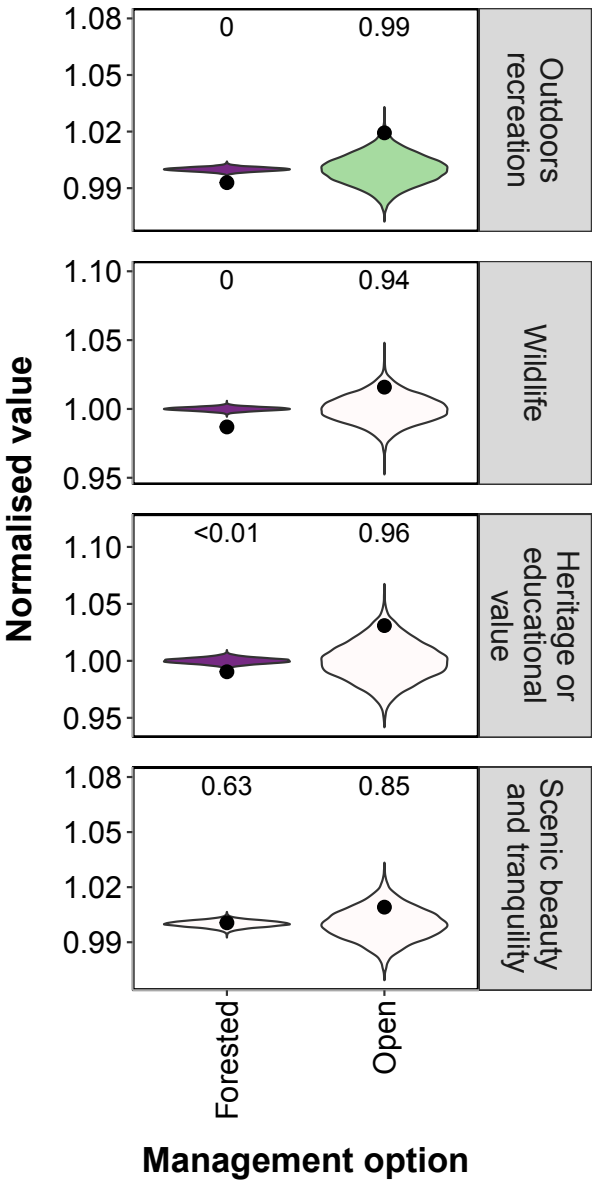

Figure 6.5: Comparison of forested areas to open space. All forested management options (conifer monocultures, conifer mixture, broadleaved monocultures, broadleaved mixture, mixed) are grouped together as 'forested'. Values from 10,000 random simulations of point data are shown as violin plots. Empirical data values are marked in relation to the violin plots by a black point. For each management option and ecosystem service combination, all values are normalised by being plotted as a proportion of the mean of the random simulations. Violin plots are scaled to have equal width across management options. As for Figure 6.4, violin plots are coloured dark green if the empirical value significantly exceeds random and dark purple if significantly lower (two-tailed); a Benjamini-Hochberg correction is calculated for each ecosystem service (see Table 6.3, methods). Plots are coloured light green or purple if the empirical values are significantly different using an unadjusted P value of 0.05 (but not with the Benjamini-Hochberg correction factor). Numbers above the plots indicate P values (the proportion of random simulations that have values lower than the value of the empirical data). Number of respondents for each ecosystem service were as follows, outdoors recreation: n = 162; wildlife: n = 101; heritage or educational value: n = 61; scenic beauty and tranquillity: n = 88.

Preferences for broadleaved species compared to conifers (hypothesis three)

Comparing broadleaved monocultures with conifer monocultures shows that, while conifers were universally very negative (recreation and scenic $P = 0.06$, wildlife and heritage both significant at $P < 0.0001$), broadleaves were only significantly negative for heritage (heritage $P < 0.0001$), and positive for recreation and wildlife ($P = 0.89$ and 0.97 respectively) (Figure 6.4). For tree species mixtures, broadleaves were not significantly negative for any ecosystem service, whereas conifers were significantly negative for recreation ($P < 0.0001$). Whereas conifer mixtures were significantly positive for scenic ($P > 0.9999$), broadleaved mixtures were significantly positive for heritage ($P > 0.99$). Overall, these results support our third hypothesis that broadleaves are preferred to conifers.

We explored these relationships further by dividing the forested land uses into finer management options (the second tier, Figure 6.6). Breaking down conifer monoculture into different species' components show trade-offs between species *(*Figure 6.6a). Whereas Corsican pine was very negative across all ecosystem services (recreation $P = 0.04$, wildlife and heritage both significant at $P < 0.0001$, scenic $P = 0.08$), all other species (with the exception of other conifer) were significantly positive for at least one ecosystem service. Of particular note, larch (*Larix* × *marschlinsii* and *Larix kaempferi*) and Douglas fir were significantly positive for recreation and wildlife (recreation: $P > 0.99$ for both; wildlife: $P > 0.9999$ for both). This is important given the different percentage compositions of these different species monocultures across the forest. Corsican pine accounts for 77.8% of conifer monoculture, whereas larch and Douglas fir monoculture combined comprise just 3.3% of conifer monoculture. As with the previous comparison between forested areas and open space, the dominance of negatively valued Corsican pine seems to have skewed the overall valuation of conifer monocultures. Similarly, the majority of broadleaved monoculture is other broadleaved species (83%). Increasing the proportion of sweet chestnut within the forest, which was significantly positive for scenic ($P > 0.9999$), may have increased the overall valuation of broadleaved monoculture. Birch, however, was significantly negative for recreation and heritage (recreation $P < 0.01$, heritage $P = 0.01$).

Deconstructing conifer and broadleaved mixtures into separate options according to whether the largest component (i.e. the species with the greatest percentage of the total species composition) was conifer or broadleaved revealed interesting results (Figure 6.6c): for heritage and scenic, mixtures dominated by a conifer were valued more positively, whereas the opposite was true for recreation and wildlife.

Preferences for mixtures compared to monocultures (hypothesis four)

Within conifers, mixtures were valued more positively than monocultures for wildlife, heritage and scenic (monoculture was significantly negative and mixture positive, though not significant, for wildlife and heritage; mixture was significantly positive and monoculture negative, though not significant, for scenic) (Figure 6.4). Interestingly, conifer mixture was negatively significant for recreation whereas conifer monoculture was not, although arguably conifer monoculture is approaching significance ($P = 0.06$) (Figure 6.4). For broadleaved species, mixtures were valued significantly positive and monocultures significantly negative for heritage (mixtures $P > 0.99$; monocultures $P < 0.0001$). Generally, mixtures were more positively valued than monocultures, supporting our fourth hypothesis, but the preference is not strong.

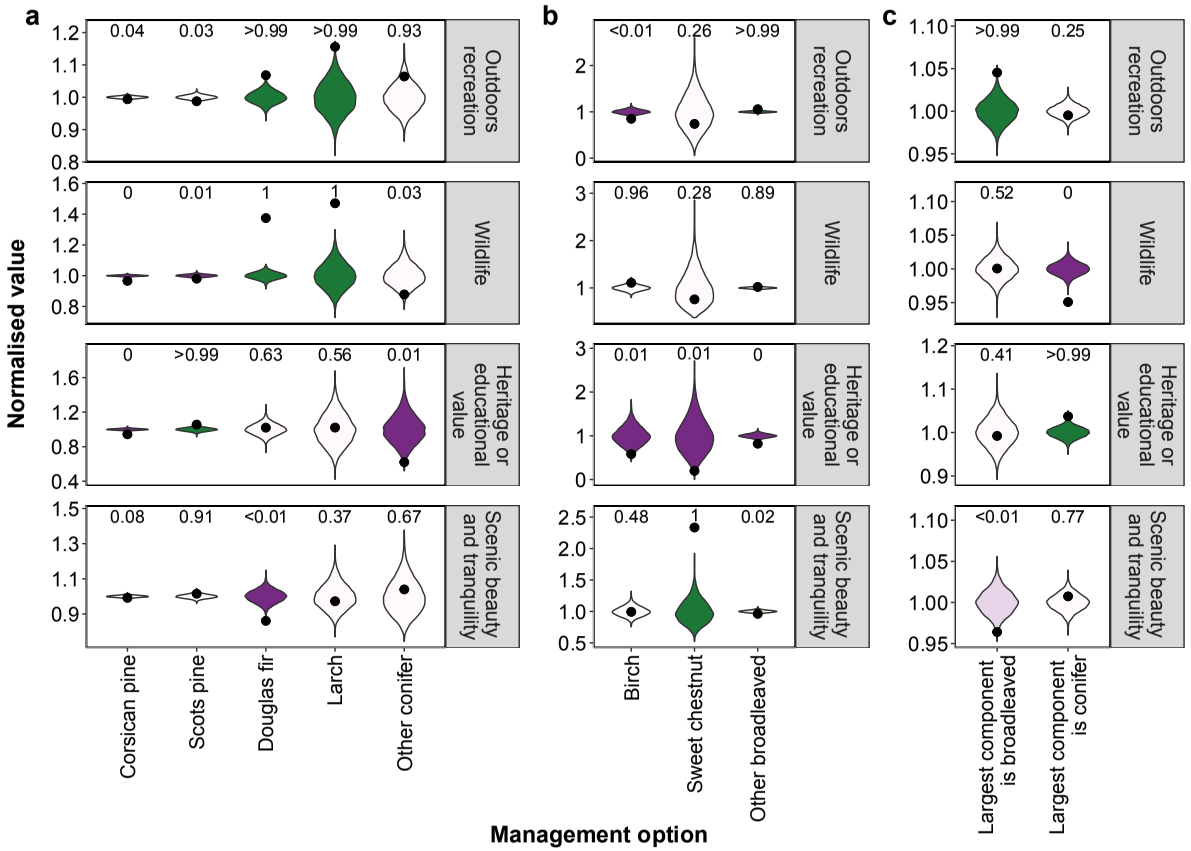

Figure 6.6: Cultural values in relation to finer management options. a) Conifer monoculture sub-options b) broadleaved monoculture sub-options c) conifer and broadleaved mixture sub-options. Values from 10,000 random simulations of point data are shown as violin plots. Empirical data values are marked in relation to the violin plots by a black point. For each management option and ecosystem service combination, all values are normalised by being plotted as a proportion of the mean of the random simulations. Violin plots are scaled to have equal width across management options. As for Figure 6.4, violin plots are coloured dark green if the empirical value significantly exceeds random and dark purple if significantly lower (two-tailed); a Benjamini-Hochberg correction is calculated for each ecosystem service (see Table 6.3, methods). Plots are coloured light green or purple if the empirical values are significantly different using an unadjusted P value of 0.05 (but not with the Benjamini-Hochberg correction factor). Numbers above the plots indicate P values (the proportion of random simulations that have values lower than the value of the empirical data). Number of respondents for each ecosystem service were as follows, outdoors recreation: n = 162; wildlife: n = 101; heritage or educational value: n = 61; scenic beauty and tranquillity: n = 88.

DISCUSSION

Our results from the Thetford Forest landscape showed that respondents had strong preferences for certain land management options even though they were not asked to consider this in the survey. A third of all broad land management and ecosystem service combinations were valued significantly positively or negatively, confirming our first hypothesis that cultural ecosystem service values vary with land management. This demonstrates the importance of land management for cultural ecosystem services and underlines the great potential to increase the delivery of cultural values from landscapes through management decisions.

Given that Thetford Forest is recognised as being an important site within the wider region, particularly for recreation, we hypothesised that visitors would prefer the forest to open landscapes. However, we discovered that the current forest composition, with a heavy bias towards monocultures (particularly Corsican pine), made the forest area as a whole valued negatively compared to open spaces (Figure 6.5). On the other hand, other species monocultures (such as Douglas fir, larch, Scots pine and sweet chestnut) and species mixtures were valued positively in different ways, with all ecosystem services valued significantly positively by at least one of these different management options (Figure 6.4 and Figure 6.6). Open space (i.e. open habitat, excluding open water) was positively valued across all ecosystem services, so it seems unlikely that forested areas will ever be preferred overall to open space within the Thetford Forest landscape. Nevertheless, these results suggest that changing the forest composition to include a greater proportion of mixtures and different species compositions could greatly increase the overall cultural value of forested areas.

In the UK, substantial areas of open habitat were afforested during the 20th century, and now a reversion of forested land back to priority open habitats is recognised as appropriate in some circumstances for biodiversity conservation [318]. The open space network within Thetford Forest supports rare plant and invertebrate assemblages, with several large heathland areas, and is designated accordingly [62]. In this study, we found that open space was rated very positively for wildlife value, although this was not significant, which is perhaps not surprising given the relatively specialist biodiversity interests. Indeed, open space was universally positive across all four cultural ecosystem services (and highly significant for recreation), probably reflecting an appreciation of open vistas in what is a relatively uniform forest landscape with little topographical change. Edwards et al. [295] found that variation between forest stands was of high importance to recreational value in Central Europe where forest density is high, but of relatively low importance in Great Britain where forest density is low, therefore suggesting that overall landscape structural diversity is key. Our findings that open space was positively valued within a largely continuous, extensive forest landscape adds support to this hypothesis. Forest openings, particularly where they are

openings of other natural habitats rather than clearfell areas (as is the case with much open space in Thetford Forest), are generally found to be valued, as are forest landscapes that offer views of surroundings [291,294]. Tyrväinen et al. [289], however, found that open views containing few trees were of low value for tourism in Finnish Lapland, although clearly expectations and preferences for habitats will vary regionally. In the Thetford Forest region, open space is clearly a highly valued component of the landscape.

Following general findings in the literature, we also hypothesised that broadleaved species would be preferred to conifers (hypothesis three) and that mixtures would be preferred to monoculture (hypothesis four). We found some evidence to support these hypotheses, although the differences were not strong. However, this corroborates the findings of Edwards et al. [319] that broadleaves and mixtures are only marginally preferable to conifers and monocultures, respectively. Furthermore, although these preferences are generally found across Europe, results are mixed [291,297,299], so it is perhaps not particularly surprising that there is not a more dramatic distinction between broadleaves and conifers or between mixtures and monocultures.

Additionally, as this methodology uses revealed preferences, these results suggest that respondents' behaviour does not reflect a strong distinction between broadleaves and conifers or between mixtures and monocultures, even if people generally claim to prefer one or the other. This reinforces the general importance of comparing people's behaviour with their stated preferences; part of the strength of this methodology is that it infers the importance of management options by asking about general values but avoids potential biases by not explicitly asking about management. Thetford Forest was established as a predominantly conifer monoculture plantation, and the initial planting of the majority of the forest is now starting to fall beyond living memory. It seems likely that respondents viewed the forest's identity as innately single-species coniferous stands. Familiarity has also been proposed as an important factor in determining people's preferences for forest attributes [295,320]; although respondents did not overall value conifers or monocultures more than broadleaves or mixtures, this may partially explain why there was less of a preference for broadleaves or mixtures than might be anticipated.

Our results also showed key differences between different tree species. Corsican pine was valued very negatively for all ecosystem services, which is unsurprising given that the majority of the Corsican pine trees within the forest are contaminated with *Dothistroma septosporum*, a fungal disease that not only renders the crop unproductive for timber, but also leads to defoliation and tree disfigurement [59]. Larch and Douglas fir were significantly positive for recreation and wildlife, and sweet chestnut for scenic beauty. This may be partially explained by their relative rarity (larch and Douglas fir account for 3.3% of conifer monocultures, sweet chestnut accounts for 1.2% of broadleaved monocultures). However, other conifers in monoculture are also very uncommon (0.9% of conifer monocultures), and these were not significantly positive for any ecosystem

services (Figure 6.6) (and were significantly negative for heritage, $P = 0.01$). There appears to be no particular distinction between native and non-native species, with mixed results for both (e.g. birch and Scots pine are native, Douglas fir is non-native). Further work to identify the exact reasons for these differences is required. Nonetheless, these results, in combination with the fact that respondents also generally valued mixtures more than monocultures, supports the proposed diversification of tree species (increasing response diversity, as well as species diversity) away from historically dominant species such as Corsican pine to improve ecosystem resilience [321,322].

Forests provide multiple ecosystem services, and tree species richness has been shown to correlate with delivery of multiple ecosystem services [46,98]. Our results generally support this, demonstrating that mixtures deliver more cultural ecosystem service value than monocultures. Additionally, as found in other studies [46], no single tree species or broad management option delivers significantly positive results – or high value – for all cultural ecosystem services. Trade-offs between ecosystem services are recorded three times more than synergies [323]. Our results underline the importance of understanding the trade-offs between different species and management options. Methods such as ours, which make trade-offs explicit, can be used to make practical management decisions that maximise the delivery of ecosystem services [324].

In landscapes such as Thetford Forest, where there is public access and high visitor use, the method has clear value in helping forest managers understand which management options are valued positively or negatively for cultural ecosystem services. The results from the analysis can contribute to future management strategies that seek to balance visitor needs against silvicultural requirements with the aim of maximising and balancing the delivery of all ecosystem services. We can make recommendations for the management of the Thetford forest landscape to increase cultural ecosystem service values. For example, we recommend the diversification of tree species used in commercial conifer planting (particularly a shift away from the dominance of Corsican pine towards species such as Douglas fir, larch and Scots pine). Open space habitats are also of great cultural importance in the Thetford forest landscape, and should be retained as a complementary management option to forestry.

The methodology described here enables the quantification and inclusion of cultural ecosystem services into land management planning by relating cultural ecosystem services directly to land management decisions. This approach has several key strengths. First, by focussing on environmental spaces as an indicator of cultural ecosystem services, the outputs will equip land managers (who do not have the time or expertise to disentangle complex human-environment relationships) with the information required to incorporate cultural ecosystem services values into practical decision-making. Second, it incorporates opinions from across all stakeholder groups in a fair and unbiased manner, ensuring high legitimacy of the results. Legitimacy has been found to be the most important factor in explaining the impact of ecosystem services science on decision-

making [325]. Third, it is the first methodology to our knowledge to develop a spatial matching technique for use with participatory GIS data (and is moreover a practical means of generally comparing multiple treatments with site matching). It allows the user to directly relate cultural values to land management while accounting for the confounding effects of landscape features. The point density maps show hotspots over the visitor centre and main recreation and heritage areas (Figure 6.3), as would be expected from knowledge of how people use the landscape. However, in our analysis we have been able to distinguish in more detail whether and how the underlying land management affects visitor preferences. This is an important step towards identifying the ecological characteristics of environmental spaces that affect cultural ecosystem services [302]. Finally, the survey is a form of revealed preference evaluation, as respondents were not told or asked about the management of the landscape. This is powerful because it incorporates preferences that respondents may not even be aware of themselves, and avoids biases.

There are a number of limitations to the methodology, which are important to bear in mind. Firstly, we did not supervise individual respondents so we could not guarantee the quality of all responses. Although we visually checked each response to ensure that there were no obviously anomalous patterns, we could not be certain that all patterns were intentional and accurate. Equally, we did not have a measure of the time that each respondent spent recording. Clearly, facilitation of surveys could decrease this uncertainty, although by using a non-supervised approach we were able to reach a wide variety of stakeholders and achieved a high number of responses from individuals who were free to complete the survey at their own convenience. Secondly, it is important to note that respondents were asked to mark areas that they positively valued, and were not asked to distinguish areas they did not like. Therefore, significantly negative results are inferred from an absence of points (significantly fewer points than would be expected from random). We believe that an absence of points is sufficient to show areas that are not valued, but future research could address this more formally using the same methodology. Thirdly, we recognise that cultural ecosystem services are co-produced by both nature and people, and therefore management interventions may have different effects on cultural values depending on the local context. Our matching technique aims to tease apart these interactions, but there may be other factors that influence cultural values besides the covariates that we have accounted for. Equally, the value of different management options will vary across different landscapes; given that our study site formed one forest landscape, we deemed it appropriate to consider management options equally across the landscape, but this should be considered in wider contexts. We set the distance class bands for covariates according to sensible thresholds for their likely influence, but this could also affect results. Finally, the localised spatial structure created by the spraycan was not fully replicated in our randomisations. However, given that the point density is so high and our compartments relatively small, and also through our matching technique, there was a high degree of spatial structure in our randomised data.

Nevertheless, this could be a consideration for refinement of the technique in future analyses. Despite these limitations and considerations, we feel that the matching technique and overall methodology presents a valuable approach to better understand how landscape management affects cultural values.

The flexibility of the methodology allows it to be applied to many scenarios across all types of landscape and management, as the landscape features and management options can be specified freely. Furthermore, as we have demonstrated with our case study, the analysis can be run at different levels of detail to reveal broad trends or to make detailed comparisons. Additionally, the ability to compare multiple treatments (rather than just a treatment and control) has relevance for other types of spatial analysis. For example, the method could be used to compare the effects of multiple conservation interventions on species abundance, while accounting for covariates. Overall, although developed to analyse cultural ecosystem service values, the site matching technique is an improvement to participatory GIS data analysis with broad multidisciplinary potential.

CONCLUSIONS

Human well-being is inextricably linked to natural capital and the provision of ecosystem services [1]. The incorporation of these concepts into decision-making processes is essential if we are to achieve future sustainability targets [250]. However, we must ensure that we consider all ecosystem services in order to achieve the greatest overall benefits, rather than focussing on a subset of well-understood services [324]. To date, cultural ecosystem services have been neglected in valuation frameworks due to their perceived intangibility. The methodology developed here shows that it is possible to ascertain, in a statistically rigorous manner, whether land management (rather than landscape features) affects cultural ecosystem service values, and it provides detailed information about trade-offs between different management options. In our case study, we have been able to use these results to make a series of forest management recommendations to increase cultural ecosystem services values. Additionally, understanding how people value landscapes at this detailed level presents an opportunity to increase engagement and connectedness to nature through changing land management at the site level. The methodology can be applied in any landscape to take local influences and viewpoints into account, and as such, it represents a significant step forward in the quantification of elusive cultural ecosystem service values.

7 | The importance of different habitat variables for bird diversity in a managed forest landscape

SUMMARY

Forest biodiversity is strongly affected by management, and commercial plantation forests have significant potential to deliver biodiversity conservation gains when managed sensitively. Although there is an expanding literature exploring how forest management affects biodiversity, most studies use simplistic measures such as species richness and there is also considerable variation in results. In this study, I explore the effects of a range of habitat variables on bird populations in an extensive forested landscape, using a variety of occurrence, taxonomic diversity and functional diversity metrics. I used high-resolution remote sensing data to quantify structural attributes at a range of resolutions. Using a combination of hierarchical partitioning analysis and linear models, I determined the relative importance of different habitat attributes and resolutions both across bird species and for diversity metrics. I also tested whether there was a significant association between individual species traits and environmental variables. Different resolutions were best for different structural variables, demonstrating the value of considering a range of scales when extracting data from remote sensing technology. Overall, habitat attributes explained very little of the total variation in bird occurrence models. However, when stands were grouped for the calculation of diversity metrics, stand age was found to be a universally significant variable; species composition, shrub density and gap fraction were also significantly associated with various metrics. Surprisingly, within-stand heterogeneity (horizontal or vertical) was not significantly associated with bird diversity. Furthermore, although I found a significant overall relationship between species traits and environmental variables, no individual pairwise interactions were significant following adjustment by a multiple-testing correction factor. The analysis took place at the scale of individual stands, which is a valuable scale for informing management decisions but does not capture wider landscape effects. From the main results of this study, especially the importance of a range of stand age classes and the lack of an effect of within-stand heterogeneity, I concluded that overall landscape heterogeneity is more important for biodiversity in a managed forest landscape than increasing within-stand heterogeneity within a homogenous wider landscape. The importance of landscape heterogeneity compared to stand heterogeneity has also been recently identified in other papers and warrants further research.

INTRODUCTION

The manner in which a forest is managed affects biodiversity [326–328]. Management strategies determine forest structure and influence resource availability, with inevitable implications for biodiversity [329,330]. For example, the size and age of trees, availability of deadwood, tree density, structural heterogeneity and tree species composition all have interrelated and important effects on a range of species [330–332]. In general, unmanaged forests support greater biodiversity than forests with timber-oriented management, but this result is highly variable, by both taxa and management strategy [327,328].

Birds are widely used as indicators of forest biodiversity [333,334]. In Europe, they are the most monitored taxonomic group; there are extensive and regularly updated data and they are relatively easy to monitor and study [334–336]. They have been found to be effective indicators of a wide variety of taxa, although results are mixed and context-specific [335,337]. There is a large body of literature focusing on the habitat requirements of forest birds, and increasingly studies focus on the effects of different management techniques and strategies [329,338]. However, knowledge gaps remain, particularly given that forest management needs to change rapidly in response to a host of unprecedented challenges, such as climate change and disease [50,283,339]. For example, shifts to uneven-aged (continuous-cover) management and the introduction of new species and mixtures are creating novel forest systems but there is a poor understanding of the effects on forest birds, and biodiversity more widely [329,340].

Forest plantations are often dismissed as 'green deserts' [341], but they have an important role to play in biodiversity conservation [342,343]. This is particularly the case when they replace degraded or intensive agricultural land, where natural forests are scarce within the landscape or plantations can improve connectivity between natural forest remnants [70,108,342–344]. Although many studies have found that plantations have a reduced bird diversity (species richness or Shannon diversity) compared to natural forests [342,345–347], a meta-analysis of studies found that species abundance was no different [348]. It is also often inappropriate to compare plantations to natural forests, given that this is frequently not a realistic alternative land use [349]. Plantations can support a wide variety of taxa, including nationally important populations of species of conservation concern, and have received conservation designations accordingly [342,345,350,351]. Structural complexity of plantations has been shown to be key in increasing species diversity and abundance, and therefore management strategies can have a profound impact [345,348,352]. Overall, plantation forests have significant potential to contribute to biodiversity conservation when managed sensitively.

In addition to the quality of forest habitat, which is determined by a combination of its structure and floristic components, there are a variety of factors that influence bird community assemblages and diversity [329,353]. For example, the climate, surrounding land uses, regional bird population sizes

and interspecific interactions all have interrelated effects [329,345,354,355]. Most existing studies exploring management effects on bird diversity in temperate forests come from North America; evidence and understanding in Europe is lacking, and given obvious intercontinental differences results cannot necessarily be extrapolated to Europe [329,330]. In particular, lowland predominantly coniferous plantations have received less attention. They are currently a relatively scarce habitat within Europe, although may increase given targets for new woodland planting and shifts to a lower carbon economy. Such plantations are important for biodiversity, particularly within a matrix of intensive alternative land uses.

Management decisions take place at the scale of a forest stand, which are areas of the same tree species composition and structure, usually a few hectares in size [356]. It is also an informative scale to study the habitat requirements of most bird species because resource use and interactions between individuals tend to occur at relatively small scales [353,357]. However, it is habitat features, rather than broad descriptions of management type or prescription, that best explain community assemblages and diversity [326]. Using remote sensing technologies, we can now measure habitat attributes in fine detail over large areas [358]. This is an opportunity to greatly increase our understanding of how forest management affects biodiversity, by determining how species respond to, and how management creates, subtle differences in habitat.

The majority of studies exploring the effects of forest management on biodiversity use metrics of taxonomic diversity, most notably species richness [327,328,359]. However, as widely recognised, this does not fully capture the multiple components of ecological communities and can be a misleading measure of biodiversity [326,360]. Therefore, approaches that include functional diversity metrics are increasingly advocated as an important complementary measure of biodiversity, both in this particular field and more generally [359,361,362].

A further key question in species distribution modelling is how species differ in their environmental responses and how species traits mediate this [363]. Species adaptations to their habitat will be reflected in their functional traits, although not all habitat features will necessarily select for these traits [364,365]. Therefore, it is informative to understand which environmental and species traits are associated that in turn will allow better predictions and understanding of how species traits drive community assembly [364,366,367]. Such information would add greatly to an understanding of how bird diversity and community assemblage is affected by forest habitat and so can be modified through management, which would potentially enable more successful targeting of conservation efforts.

In this study, I explored how forest habitat attributes affect bird biodiversity in a large commercial plantation in the UK lowlands. I used high resolution remote sensing data and a variety of taxonomic and functional diversity metrics to investigate how forest management affects different

biodiversity components. I also explored whether it is possible to detect associations between environmental and species traits.

METHODS

Study site

Thetford Forest is a large plantation (18,719 ha) in East Anglia, UK. Although there were some existing woodlands in the region, the majority of the forest was planted after the First World War as part of a national afforestation strategy. It is largely coniferous, although there are areas of broadleaved and mixed woodland, and significant areas of open heathland within the forest matrix. Thetford Forest is an important biodiversity site, being designated as a Site of Special Scientific Interest for its breeding populations of nightjar and woodlark and its invertebrate and plant assemblage [62]. It is also part of the Breckland Special Area of Conservation as well as the Special Protection Area [63,64].

Bird and spatial data

Bird surveys (completed by the BTO – see Preface) took place in early summer in 2015 and 2017, following the UK Breeding Bird Survey methodology. The forest was divided into 1-km squares, of which 57 were randomly selected in 2015 and 76 in 2017. Two transect lines were drawn across each 1-km square, 250 m from opposite boundaries. The exact transect line route varied from the 'ideal' route due to habitat permeability and access, although each transect was 150 m apart wherever possible. Field surveys took place between 6 and 11 am. The transects were walked by an observer at a slow to medium pace with all birds seen or heard within 250 m of the transect recorded on a 1:2500 scale, detailed forest map. Each 1-km square was visited twice, with at least two weeks between visits. The bird observations were then grouped by forest subcompartment, and the maximum count of the two visits used for analysis. Maximum count, rather than mean, is the standard used for Breeding Bird Surveys as it provides a pragmatic way of dealing with replication within counts and if areas are covered in more than one transect (for example, some subcompartments were split over different transects).

Each forest subcompartment is a unit of forest management, with detailed management information attributed to it, such as tree species composition and age classes. Remote sensing data used to calculate structural information (see below) was available for only part of the forest in the two survey years, so I retained only the corresponding 1-km bird survey squares for analysis. This left 51 1-km squares covering 1,658 subcompartments in 2015 and 16 1-km squares covering 443 subcompartments in 2017 (with no overlaps between years). For analysis of structural data, I clipped subcompartment shapefiles to the edges of the survey area (250 m from each transect line).

I attributed a management type to each subcompartment according to common management practices across the forest (for example, conifer monoculture, conifer and broadleaved mixture, open space). This was determined using the detailed Forestry Commission subcompartment database. Similarly, I assigned an age class to each subcompartment that contained trees according to forestry convention (for example restock, thicket, mature, felled). Slight differences between geospatial datasets used for bird surveys and the management database resulted in some exclusions of subcompartments where management could not be accurately identified (61 in 2015, 12 in 2017). Finally, I excluded subcompartments if the area falling inside the survey area was less than 0.05 ha (65 in 2015, 16 in 2017).

I built a trait database for the bird species observed using various literature sources (Appendix table F.1).

LiDAR

To quantify structural attributes for each subcompartment, I used airborne Light Detection and Ranging (LiDAR) remote sensing data. LiDAR generates a point cloud of ground, vegetation and object heights using a laser scanning technique. I used LiDAR point cloud data generated from flights in February and March in 2015 and 2017. Different areas of the forest were covered in the two different years, with no overlap. Firstly, point returns were classified as ground or non-ground points, which enabled the production of a digital elevation model. The heights of the points were then normalised with respect to the digital elevation model. A pit-free canopy height model was produced from the normalised point cloud at a resolution of 0.5 m. All initial processing used LAStools algorithms [368].

In addition to the canopy height model, a vertical plant area distribution profile was produced at a resolution of 10 m. This approach is based on the MacArthur-Horn method (developed to estimate foliage profiles in the field), and adapted for use with LiDAR data [369–372]. For each 10-m square, the point cloud was split into 1-m vertical segments and the plant area distribution (PAD) calculated as the log of the fraction of points intercepted within the 1-m segment:

$$PAD_i = \frac{1}{\Delta z} ln\left(\frac{n(k = 1, z \leq z_1)}{n(k = 1, z \leq z_2)}\right)$$

Where, z_1 is the upper height of the vertical segment i, z_2 is the lower height of the vertical segment i, $\Delta z = |z_2 - z_1|$ (i.e. 1 as this was calculated for 1-m segments), $n(k = 1, z \leq z_1)$ is the number of returns entering the top of the segment, $n(k = 1, z \leq z_2)$ is the number of returns penetrating through the segment to lower vertical segments [370]. This method assumes that vegetation is randomly distributed within each vertical segment. Other studies deal with issues of canopy clumping by applying a scalar correction factor to more accurately predict true leaf area density

[370,371]; however, this is an unknown constant and there are no available estimates from a similar managed forest system, so a scalar correction constant was not used. Applying a correction factor would not affect my conclusions unless a constant was applied differentially across the landscape, for example for different habitat types. The calculated plant area distribution values therefore represent an effective intercepting value rather than a true estimate.

From the processed canopy height model and plant area distribution profile, I derived six metrics to describe the habitat structure: top canopy height, gap fraction, horizontal heterogeneity, vertical evenness, shrub density and canopy density (Table 7.1). Firstly, by taking the mean pixel value, I aggregated the canopy height model into different resolutions: 0.5 m, 2 m, 5 m, 10 m and 50 m. For each of these five resolutions, I extracted the corresponding pixels for each subcompartment (pixels were selected when their central point was within the subcompartment). Similarly, I separated the plant area distribution profile by subcompartment, and calculated the mean value of each vertical segment. For each subcompartment I extracted the mean plant area distribution values of a segment if $i \leq I_{max}; I_{max} = round[tch + (2 \times SD_{tch})]$, where i is the vertical segment, tch is the mean top canopy height for the subcompartment calculated at the 10 m resolution (to match the resolution of the plant area distribution data), SD_{tch} is the standard deviation of the top canopy height for the subcompartment at the 10 m resolution, and $round$ indicates the value is rounded up to the nearest integer. This captured the majority of the variation in top canopy height across the subcompartment, and excluded any erroneous values from above the canopy as a result, for example, of bird hits in the LiDAR point cloud. The calculations of each structural metric are detailed in Table 7.1. For canopy density calculations, I calculated the top third of the canopy (I_{canopy}) as $round\left[\frac{2\times[tch+(2\times SD_{tch})]}{3}\right] \geq I_{canopy} \leq I_{max}$. Values below 1 m were originally used as a calculation of field layer density, but I later excluded this from analysis due to uncertainty in values of plant area distribution at low height levels.

Table 7.1: Structural metrics calculated from the LiDAR data. The plant area distribution values are the extracted values as explained in the text (vertical segments less than the top canopy height + 2SD for each subcompartment).

Structural metric	Processed LiDAR data used	Resolution(s) (m)	Calculation for each subcompartment
Top canopy height	Canopy height model	0.5, 2, 5, 10, 50	Mean pixel value
Gap fraction	Canopy height model	0.5, 2, 5, 10, 50	Percentage of pixels that were less than 2/3 of the mean top canopy height value
Horizontal heterogeneity	Canopy height model	0.5, 2, 5, 10, 50	Moran's I index of all pixel values
Vertical evenness	Plant area distribution values	10	Pielou's index (Shannon index divided by logarithm of the number of observations)
Shrub density	Plant area distribution values	10	Sum of plant area distribution values in vertical segments above 1 m and below 5 m in height

Canopy density	Plant area distribution values	10	Sum of plant area distribution values in vertical segments in the top-third of the canopy

Statistical analysis

Individual subcompartments

Prior to analysis I removed 72 subcompartments that had incomplete structural information (for example if there were gaps in the LiDAR point cloud or the mean top canopy height was below 1 m). Firstly, I analysed data at the level of individual subcompartments; due to very low, zero-inflated counts at this resolution I converted count data to presence/absence data. As subcompartments varied in size, I separated subcompartment area into two variables according to distance from the transect: near (<25 m) or far (>25 m). 0-25 m is the first distance band in the Breeding Bird Survey and is the distance class for which there is a high degree of bird detectability; beyond 25 m detectability is compromised, particularly in thick vegetation such as forest. I tested whether taking the log of these area variables improved model fit by comparing binomial linear models that contained just the untransformed near total area and far total area variables with models that contained the log-transformed area variables. For a wide variety of species (both rare and common), the log-transformed area terms had a consistently lower residual deviance and smaller Chi-squared statistic calculated using the Hoslem test; I therefore used the log-transformed data.

I used hierarchical partitioning to determine the relative importance of different structural and management variables in describing bird species presence/absence. Hierarchical partitioning attributes goodness of fit measures for multivariate regression to individual variables and calculates the independent and joint contribution of each variable (where joint contributions are effects that are caused jointly with other variables) [373,374]. Hierarchical partitioning is an attractive analytical technique because it can deal with multicollinearity between independent variables [375]. I limited the number of variables to nine, as this is the maximum for which the R function can accurately calculate individual variable statistics [375,376]. I calculated the hierarchical partitioning of different variables for every bird species observed in at least 15 subcompartments across the forest (see Appendix table F.1 for species counts), using a binomial model and R^2 as the goodness of fit measurement. For each species, I calculated the overall percentage of both the independent and joint effects for each variable (the individual contribution multiplied by 100, divided by the sum of all independent and joint contributions; joint components could be negative), and the rank of each variable as determined by the percentage of independent effects (where 1 is the highest rank, corresponding to the highest percentage of independent effects). For every variable, I then calculated the overall mean percentage of independent effects and mean rank across all bird species.

As the top canopy height, gap fraction and horizontal heterogeneity structural variables were all calculated at a range of resolutions (0.5 m, 2 m, 5 m, 10 m and 50 m), I initially used hierarchical partitioning to determine which resolution was best for each variable. A resolution of 50 m could not be calculated for some small subcompartments, so I calculated hierarchical partitioning separately for firstly, all subcompartments testing resolutions up to 10 m, and secondly, for the subset of subcompartments that had resolutions up to 50 m. I selected the 'best' resolution as the resolution that had the lowest mean rank, calculated across all species. In addition to these three variables, I included vertical evenness, shrub density, canopy density, the broad management type (conifer, broadleaved, mixture or open/other), the log-transformed total near area and log-transformed total far area to complete the nine independent variables, and ran the hierarchical partitioning on these variables across the different species. I summarised the data as boxplots and calculated the mean independent effects percentage and mean rank for each variable. Finally, I also calculated these summary statistics separately for bird species according to their UK conservation status (green- versus red/amber-listed) and their migratory status (resident versus partial/full migrant), in order to assess whether the variable importance shifted according to different bird groups of interest. To test whether variable was a significant predictor of either the percentage of independent effects or the rank, I used a repeated measures type 3 ANOVA with species as a random effect. I checked whether the sphericity function for each model was met and used the Greenhouse-Geisser corrected *P* value where it was not.

Grouped data

In addition to analysis at the individual subcompartment level, I summarised data across multiple subcompartments to compare bird community assemblages that were found in different habitat types. I grouped subcompartments according to their forest management type: Corsican pine monoculture, Scots pine monoculture, Douglas fir monoculture, 'other' conifer monoculture, conifer mixture, birch monoculture, 'other' broadleaved monoculture, broadleaved mixture, mixture (primary component is conifer), mixture (primary component in broadleaved), open, open with trees, other and felled. I then subdivided these according to age class: restock (0-6 years), pre-thicket (7-11 years), thicket (12-21 years), pole (22-45 years), mature (46 years +), mixed ages, not applicable (i.e. open/other). I then excluded groups with fewer than 10 subcompartments, which resulted in a total of 31 groups. For each group, I calculated the mean maximum count for each bird species across the subcompartments in that group. To account for detectability differences between birds, and the effects this has on community composition, I divided the mean count by a species-specific detectability constant calculated from UK-wide Breeding Bird Survey data (calculated for birds at 100 m) [377]. The detectability constant obviously cannot multiply up species counts that are zeros, but the amalgamation of data across multiple subcompartments reduced the overall

prevalence of zeros and so this was deemed to be an improvement on the raw abundance data to account for detectability differences between species.

For each group, I then calculated a variety of diversity metrics: species richness, species diversity, functional richness, functional evenness, functional divergence and functional dispersion. For calculation of functional diversity, I included species-specific trait information on body mass, migratory status, nest site, diet and foraging strata (Appendix table F.1). I tested the normality of these metrics using the Shapiro Wilk test: species richness, functional evenness, functional divergence and functional dispersion were all normally distributed; functional richness was highly skewed ($P = 3.75\text{x}10^{-6}$) while species diversity was borderline ($P = 0.056$). I therefore used Box-Cox transformations for both functional richness and species diversity, finding the best lambda parameter using profile log-likelihoods. For each group, I summarised the structural data calculated from the LiDAR by taking the mean value and calculating the total area of all subcompartments in each group. To determine the relationship between total area and each of the diversity metrics, I randomly sampled subcompartments from within the largest group (Corsican pine monoculture, pole age class) and calculated total area and every diversity metric for each sample community. I took 2,700 samples from the group (randomly sampling between 10 and 250 subcompartments, increasing by a multiple of 10, each 100 times), and then took the average mean counts across all species for every sample. The linear relationship between total area and each metric (transformed to match the raw data where appropriate) was greatly improved by log-transforming total area (Appendix figure F.1).

To determine the relative importance of different variables in predicting each of the diversity metrics, I again used hierarchical partitioning. For the individual subcompartment analysis, I first determined which resolution was best for each of top canopy height, gap fraction and horizontal heterogeneity. In addition to these three variables, I included broad management type, age class, vertical evenness, shrub density, canopy density and (log) total area. I expected various variables to be colinear (such as age and top canopy height) so I checked this formally by running pairwise correlation tests between different variables (Pearson's correlation between two continuous variables, R from the linear model between a continuous and categoric variable, Cramer's V between two categoric variables). As is conventional practice, I set a collinearity threshold of |0.7|, and from this determined which sets of variables were independent (see *Appendix table F.2* for results). From the results of the hierarchical partitioning, I selected, for each of the six diversity metrics, the set of variables that were independent and contributed the greatest overall percentage of independent effects to the model goodness of fit. Finally, I built a separate linear model including the selected variables for each diversity metric and checked the distribution of residuals. I assessed the overall model significance and the significance of each variable using a type 2 ANOVA. As well as determining the overall significance of the variable, for the categorical variables broad

management type and age class, I compared each category to a baseline of 'conifer' and 'mixed ages', respectively.

Trait-environment relationships

Analysing how environmental trait and species traits are associated is generally known as the fourth-corner problem, involving the simultaneous analysis of three tables detailing 1) species abundance by site, 2) a species trait database, 3) a site environmental traits database, to find the fourth 'corner' interaction between species traits and the environment [363,366,378]. Many methods have been proposed to achieve this, broadly classified as regression-based or correlative [363,378–384]. This research area is progressing rapidly, with testing of different techniques revealing inflated type I error problems (for example due to the resampling or permutation technique, or if the models miss important traits) [364]. Therefore, despite the attraction of regression-based techniques (which can give information on both the significance of an association and its strength), I explored trait-environment associations using complementary correlative approaches that effectively control type I error rates [363,380].

I used a combination of RLQ and fourth-corner analysis [380]. Firstly, I used RLQ analysis to determine whether there was an overall association between traits and environment (see Appendix table F.1 for traits). Following Dray et al. (2014) [380], I performed a separate ordination on three tables: environmental (site by environmental data; R), community (site by species abundance; L), traits (species by trait, Q). The analyses of the three tables were then combined and two permutation analyses run, one permuting sites and one permuting species, to test for relationships between the environment and species distribution or between species traits and species distribution. To control for the type I error, following guidance in recent literature [364,378,380], I used the P_{max} test, which combines the two permutation analyses and takes the maximum P value of both as the overall statistic. Assuming a significant relationship, I then used a fourth-corner analysis to test for pairwise significant associations between traits and environment. Finally, I applied a Benjamini-Hochberg correction to the fourth-corner analysis to correct for multiple testing. For both the RLQ permutation tests and fourth-corner analysis, I used 49,999 repetitions to ensure high statistical power. I performed analysis at both the level of individual subcompartments and the grouped data.

R packages

All analysis was performed in R. Specific packages used were 'raster' (general spatial), 'ResourceSelection' (Hoslem test), 'hier.part' (hierarchical partitioning), 'car' (ANOVA statistics), 'vegan' (Shannon diversity index), 'FD' (functional diversity metrics), 'MASS' (Box-Cox transformation), 'DHARMa' (model checking and residual simulations), 'ade4' (RLQ and fourth-corner analysis) [376,380,385–393].

RESULTS

Spatial and structural data

The mean subcompartment area was 2.35 ha (±2.53 sd), ranging from 0.053 to 15.77 ha. Mean top canopy height was 8.95 m (±5.60 sd), with a maximum height of 24.79 m. Different resolutions of top canopy height were generally similar (normally within a few decimal places) as they were aggregating means at different levels (Figure 7.1). The mean gap fraction and horizontal heterogeneity decreased with increasing resolution size. This is because diversity in pixel values decreased with increasing resolution size as original values were aggregated; horizontal heterogeneity therefore decreased and similarly the percentage of pixels with values below the gap fraction threshold also decreased. There was a full range of values observed for vertical evenness, although the majority of subcompartments had high vertical evenness. Shrub density was generally low across subcompartments; similarly, the majority of subcompartments had relatively low canopy density, although there was higher variation than for shrub density (Figure 7.1).

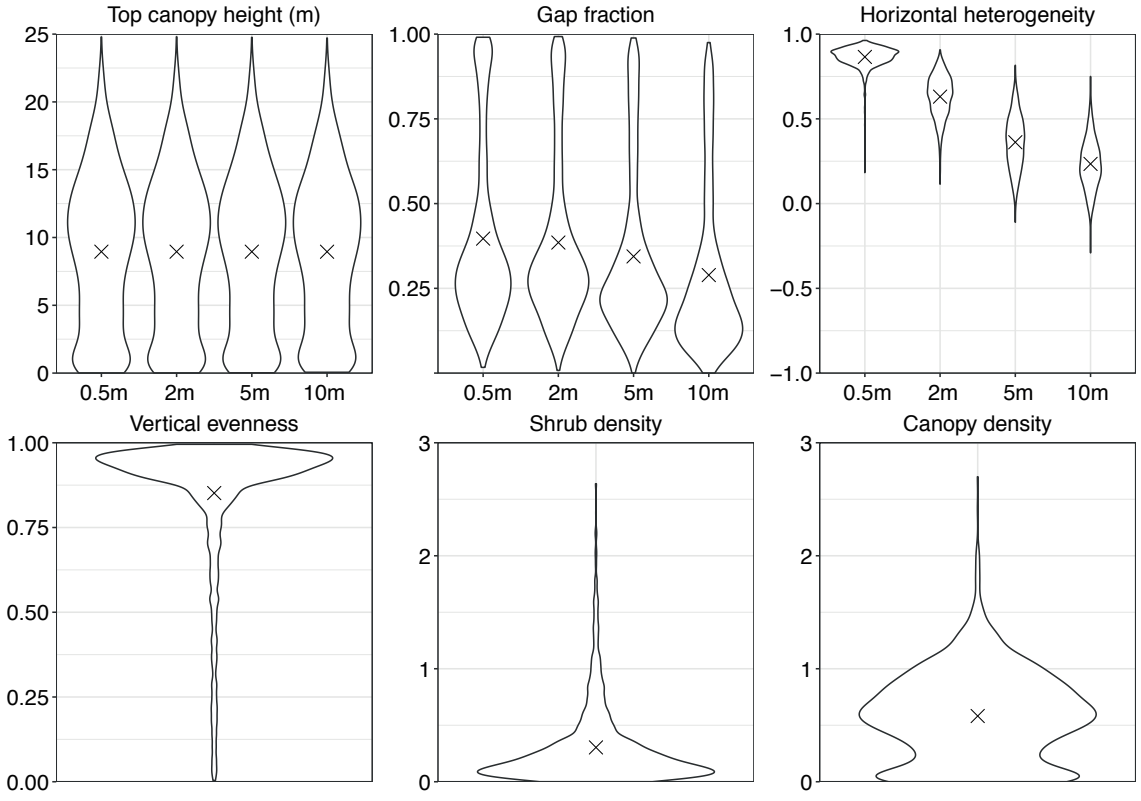

Figure 7.1: The variation in structural characteristics derived from the LiDAR data. The violin plots show the variation across all subcompartments. Crosses indicate the means. The structural metrics in the top row were calculated at different resolutions and data are shown for each of these resolutions accordingly (the 50 m resolution is not shown as some subcompartments were too small for data to be calculated at this resolution). The structural metrics in the bottom row were derived from the plant area distribution values at one resolution (10 m). Note that the y-axis differs across the six graphs.

Bird observations

48 bird species were observed, of which 35 had more than 25 observations and 17 had over 100. The mean number of observations was 166.4. Wren *Troglodytes troglodytes* was the most observed species (1,271 observations), with almost double the number of counts of the next most numerous species (robin *Erithacus rubecula*: 675 observations). Curlew *Numenius arquata* was the rarest species, with just one observation. Appendix figure F.2 gives further details.

Individual subcompartments – presence/absence of different species

Hierarchical partitioning – resolutions of structural variables

For all variables and both groups (up to 10 m or up to 50 m), the largest resolution (10 m or 50 m, respectively) had the highest mean percentage of independent effects (Figure 7.2). The largest resolution also had the lowest mean rank for horizontal heterogeneity across both groups, top canopy height for up to 10 m, and gap fraction for up to 50 m. The 5 m resolution had lowest mean rank for gap fraction in the up to 10 m group, and the 0.5 m resolution tied with the 50 m resolution for the lowest mean rank for top canopy height in the up to 50 m group. Given that only resolutions up to 10 m existed for all subcompartments, in the final variable selection I therefore used a resolution of 10 m for horizontal heterogeneity and top canopy height and a resolution of 5 m for gap fraction.

The resolution was a significant predictor of the percentage of independent effects and rank for horizontal heterogeneity in both the up to 10 m group ($P = 2.43 \times 10^{-11}$ and $P = 4.63 \times 10^{-12}$, respectively) and the up to 50 m group ($P = 6.23 \times 10^{-10}$ and $P = 1.22 \times 10^{-16}$, respectively). Resolution was also a significant predictor of the percentage of independent effects for gap fraction in the up to 50 m group ($P = 4.56 \times 10^{-4}$).

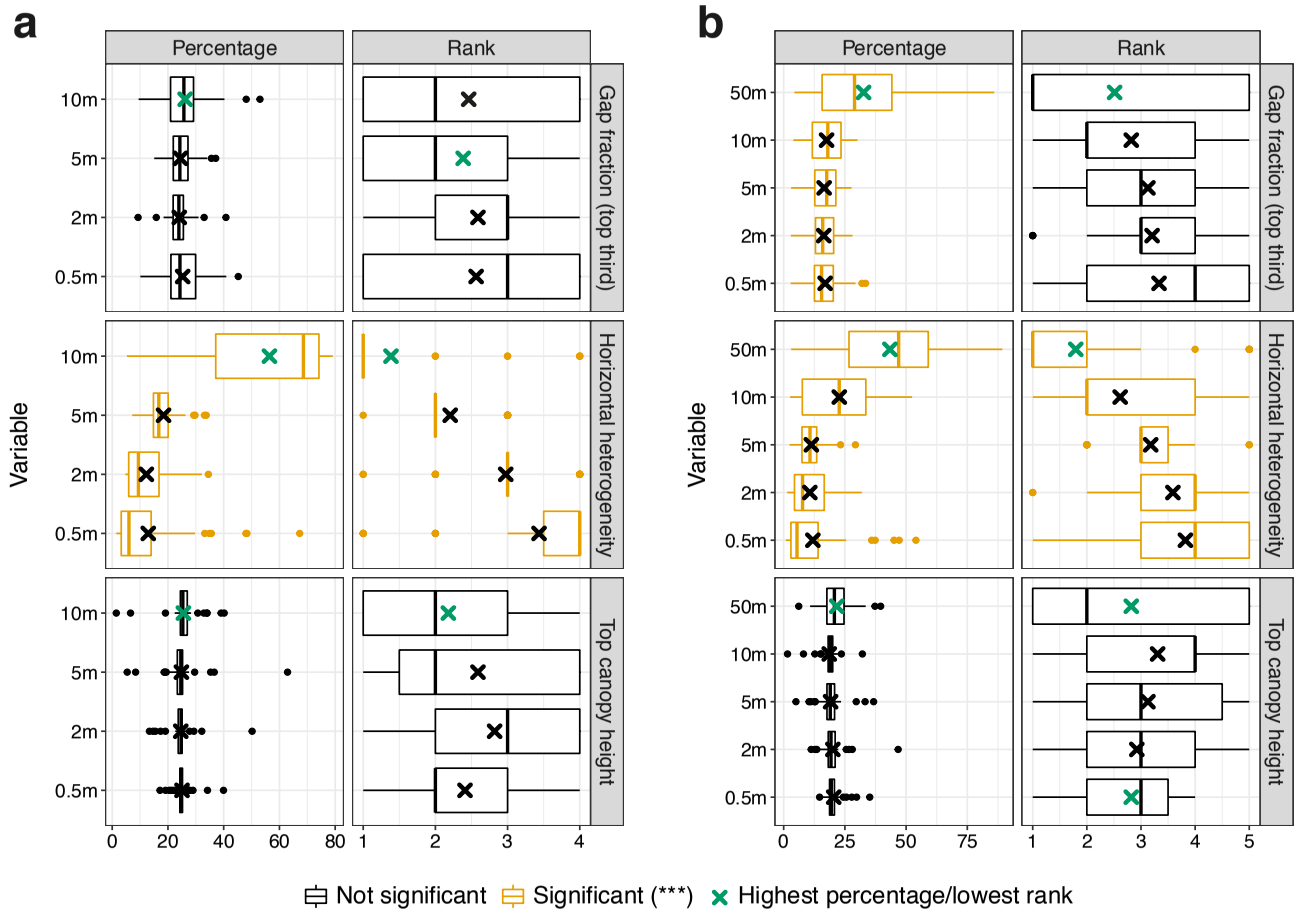

Figure 7.2: Hierarchical partitioning of different resolutions of structural variables. The percentage of independent effects and ranks of a) all subcompartments, b) only subcompartments that have resolutions up to and including 50 m. Lower rank values are better than higher rank values. Boxplots show variation across all species; the bold vertical line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles, whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Crosses indicate the mean value across species. Points indicate values that are beyond the whiskers. The green cross indicates the resolution that has the highest percentage or lowest rank for that variable. Yellow boxplots indicate that the resolution variable was a significant predictor of the percentage of independent effects or rank.

Hierarchical partitioning – final nine variables

Variable was a highly significant predictor for both percentage of independent effects ($P = 8.54 \times 10^{-20}$) and rank ($P = 6.66 \times 10^{-24}$). Subcompartment areas near (<25 m) to the transect had the highest mean percentage of independent effects and the lowest mean rank, followed by subcompartment areas far (>25 m) from the transect (Figure 7.3). The two area variables also had the highest joint percentage effects. All other variables had fairly similar independent and joint percentage effects, and higher variation in rank. Broad management type, gap fraction and top canopy height had the next lowest mean ranks after area; shrub density had the lowest mean rank overall. However, all variables had fairly low absolute values of independent effects (i.e. the R^2 attributed to each variable). 'Area near' contributed 0.036 of the total variation while 'area far' contributed 0.024. All other variables contributed less than 0.01; shrub density contributed the least (0.0028).

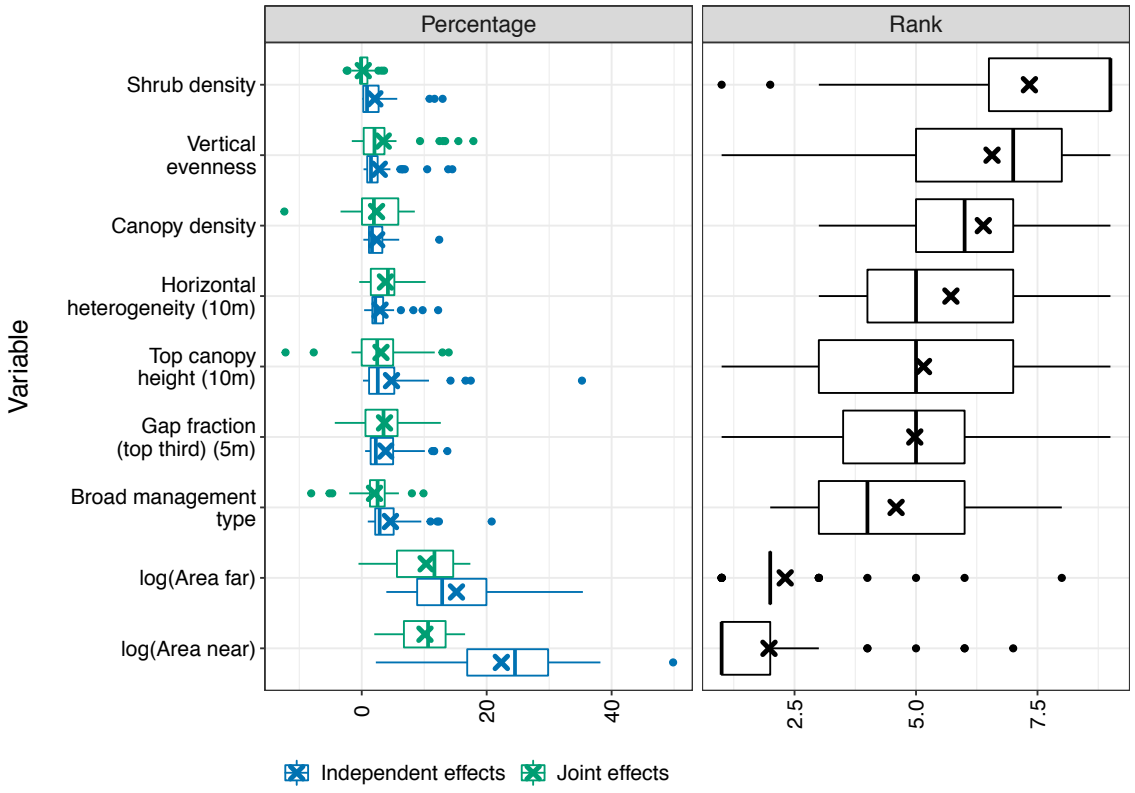

Figure 7.3: Hierarchical partitioning of the final nine variables. The left panel shows the percentage of independent and joint effects for each variable, the right panel shows the rank of the variable according to its independent effects. Variables are ordered by rank. Lower rank values are better than higher rank values. Boxplots show variation across all species; the bold vertical line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles, whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Crosses indicate the mean value across species. Points indicate values that are beyond the whiskers.

Hierarchical partitioning – final nine variables, separated by trait data

When bird species were separated by conservation status (green or red/amber), variable was a significant predictor for percentage of independent effects (green: $P = 2.11 \times 10^{-17}$; red/amber: $P = 5.88 \times 10^{-4}$) and for rank (green: $P = 1.79 \times 10^{-18}$; red/amber: $P = 1.10 \times 10^{-7}$). Area variables remained the most important, although curiously the 'area far' variable was the most important by rank for red/amber species, as opposed to the 'area near' variable (Figure 7.4). The order of ranked variables for green conservation status bird species was largely the same as when all bird species were included (except top canopy height and horizontal heterogeneity) (Figure 7.3 and Figure 7.4). However, for red or amber conservation status bird species, top canopy height was the most important variable after area, and horizontal heterogeneity was the least important (tied with shrub density) (Figure 7.4).

When bird species were separated by migratory status, variable was also a significant predictor for percentage of independent effects (resident: $P = 4.16 \times 10^{-17}$; migratory: $P = 7.18 \times 10^{-4}$) and for rank (resident: $P = 8.34 \times 10^{-21}$; migratory: $P = 8.07 \times 10^{-4}$). The area variables still explained the most variation in the models (Figure 7.4). Similarly to the results for green conservation status species, resident bird species followed largely the same order of variable importance when all bird species were included (horizontal heterogeneity and gap fraction were swapped in mean rank order, although variance was large) (Figure 7.3 and Figure 7.4). However, for migratory species, gap fraction had a larger mean independent effects percentage, making it higher ranked than broad management type. Horizontal heterogeneity became the second lowest rank (Figure 7.4).

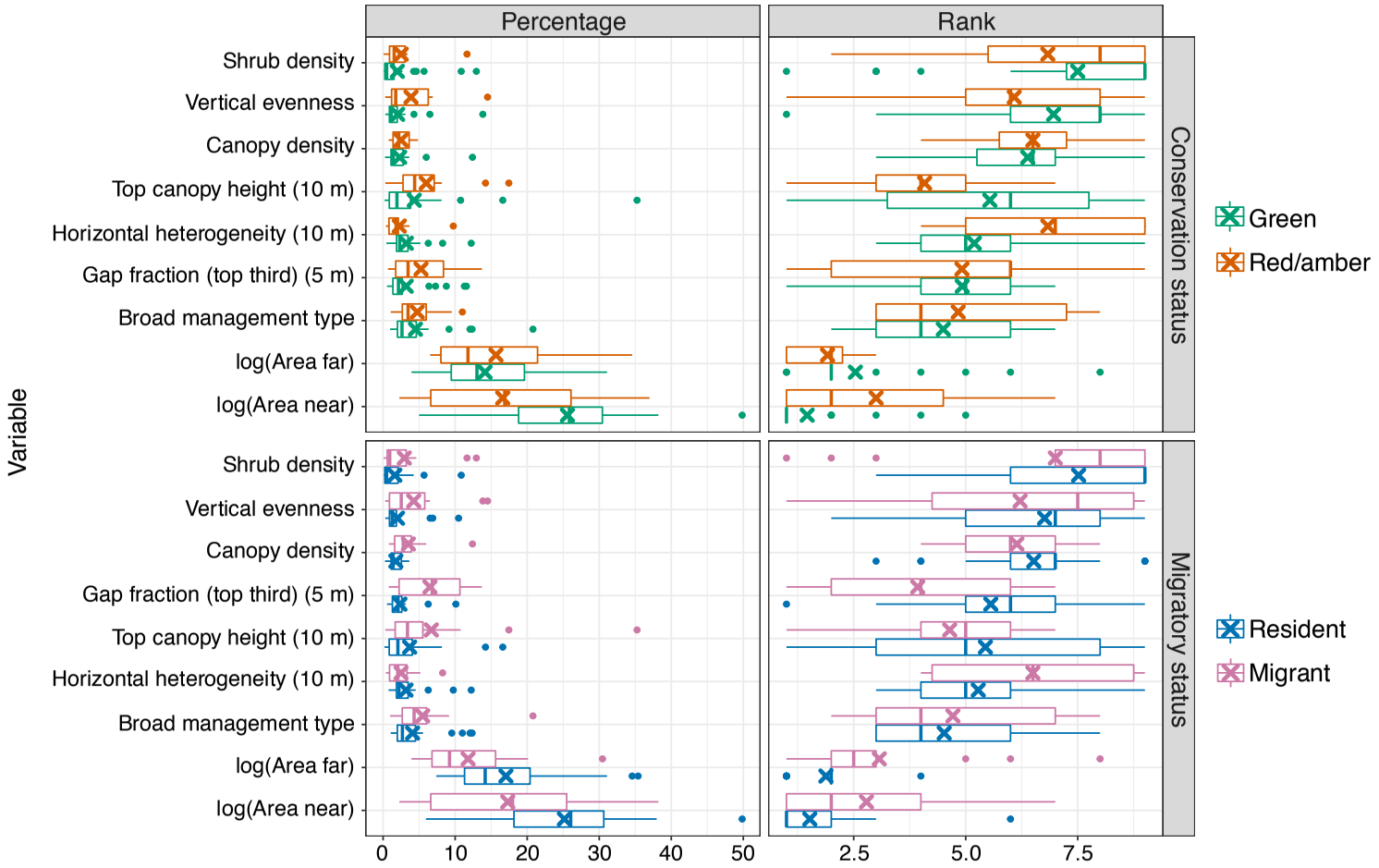

Figure 7.4: Hierarchical partitioning of the final nine variables, with species separated according to UK conservation status or migratory status. The left panels show the percentage of independent and joint effects for each variable, the right panels show the rank of the variable according to its independent effects. Lower rank values are better than higher rank values. Variables are ordered by the rank of green conservation status species (top panel) or the rank of resident species (bottom panel). Boxplots show variation across all species; the bold vertical line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles, whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Crosses indicate the mean value across species. Points indicate values that are beyond the whiskers.

Grouped data

Different resolutions

A different resolution had the lowest mean rank for each variable: 0.5 m for gap fraction, 10 m for horizontal heterogeneity, 5 m for top canopy height (Figure 7.5). Percentage effect values are not presented in Figure 7.5, as for some variables the total summed effect size from both joint effects (which can be negative) and independent effects approached zero, which vastly overinflated percentage calculations. I also did not calculate a *P* value for the effects of variables on rank, as it was not possible to check sphericity assumptions (because a singular sum of squares and products matrix was produced in the repeated measures ANOVA).

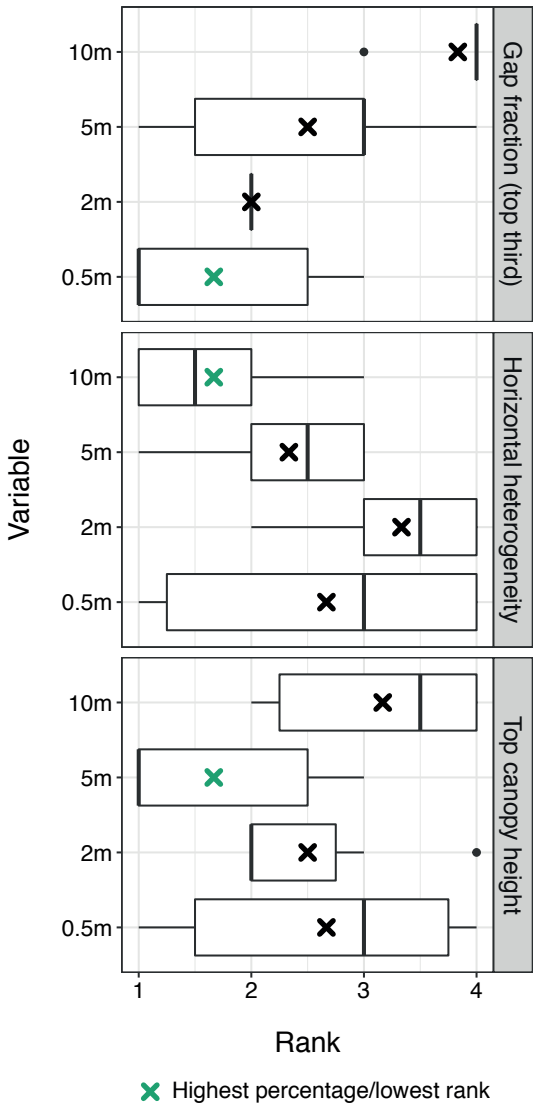

Figure 7.5: Hierarchical partitioning of different resolutions of structural variables. Lower rank values are better than higher rank values. Boxplots show variation across all diversity metrics; the bold vertical line corresponds to the median, the upper and lower hinges correspond to the 1st and 3rd quartiles, whiskers extend to the largest value that is no more than 1.5 times the interquartile range from the closest marked quartile. Crosses indicate the mean value across diversity metrics. Points indicate values that are beyond the whiskers. The green cross indicates the resolution that has the lowest rank for that variable.

Hierarchical partitioning – final nine variables

Alongside gap fraction (0.5 m), horizontal heterogeneity (10 m) and top canopy height (5 m), I included broad management type, age class, vertical evenness, canopy density, shrub density and log total area as variables for hierarchical partitioning for each of the grouped outputs. These variables accounted for between 76% (functional divergence) and 94% (species richness) of the total variation in the data. The quality of functional richness given by the dbFD function was 0.95, and the dimensionality reduction required was 36 out of 47 axes.

For species richness, species diversity (Shannon index), functional richness and functional evenness, total area had the greatest percentage of independent effects, followed by age class (Figure 7.6). Total area accounted for by far the greatest explained variability, particularly for species richness ($R^2 = 0.7$) and functional richness ($R^2 = 0.63$). In contrast, for functional divergence and functional dispersion, area accounted for just 1% of explained variability and was the penultimate least important variable, although age class remained important (Figure 7.6). In terms of the patterns of variable importance and effect size, species richness and functional richness were very similar as were functional divergence and functional dispersion, indicating that each of these pairs was influenced in the same way by the structural variables.

For all dependent variables, shrub density, broad management type and horizontal heterogeneity each accounted for less than 8% of the explained variability. However, as they were not collinear with age class or total area, and also given the general importance of age class and total area, these variables were present in the final model. Canopy density, top canopy height and vertical evenness were dropped from the final models as they were collinear with age class or total area. These variables did not account for more than 14% of the explained variability.

Total area, age class, horizontal heterogeneity, broad management type and shrub density were the independent variables chosen for all the diversity metrics except functional dispersion, when gap fraction was chosen instead of total area. The total independent effects explained by these final models was just 29% for functional divergence and 34% for functional dispersion. However, the variables for all the other models explained at least 64% of the variation; for species richness the independent variables explained 87% of the variation.

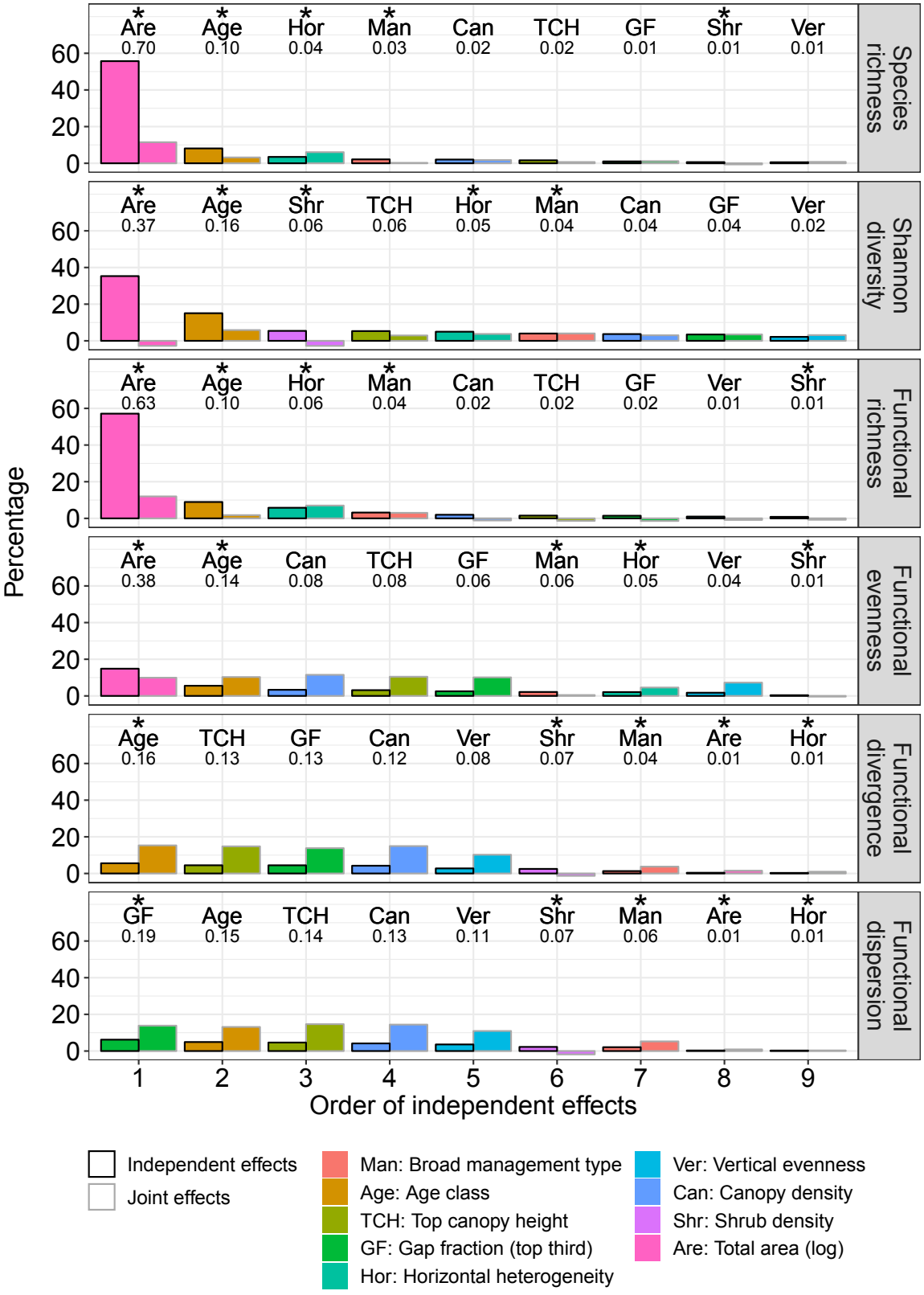

Figure 7.6: Hierarchical partitioning of the final nine variables for grouped data, for each of the six diversity metrics. Bars show the percentage of independent and joint effects attributed to each variable. Variables are ordered by the rank of independent effects. Bars are colour-coded by variable, and three-letter codes above bars aid interpretation (see legend). Values above each bar are the absolute values of independent effects, i.e. the R^2 attributed to each variable. Asterisks indicate the variables included in the final linear model, i.e. the combination of variables that are not collinear that explain the highest amount of variation.

Linear model outputs (table and graphs)

The linear models for each dependent variable were all significant (all $P < 0.002$). Model residual checks confirmed that all models met assumptions. Age class was a significant predictor for all models (except functional dispersion, where it is not included); total area was a significant predictor for all dependent variables except functional divergence and functional dispersion (Table 7.2). Species richness, species diversity and functional richness increased with total area, while functional evenness decreased with total area (Table 7.2 and Figure 7.7). The thicket/pole age class had significantly lower values than the mixed age class for species richness, species diversity and functional richness, and significantly higher values of functional evenness. Additionally, the restock/pre-thicket and not applicable (i.e. open space) age class had significantly higher values of functional evenness and functional divergence.

Shrub density was significantly associated with species diversity and functional dispersion, although the increase was marginal over the range of values observed in the forest (0.02 – 1.09) (Table 7.2 and Figure 7.8). Gap fraction was also a significant predictor of functional dispersion and had a greater effect on predicted values (more than 2.5 times increase in gradient) (Table 7.2 and Figure 7.8). Finally, management type was significantly associated with functional evenness; mixtures and open/other had significantly higher functional evenness than conifers (open/other was almost 3 times the degree of increase compared to mixture) (Table 7.2 and Figure 7.8).

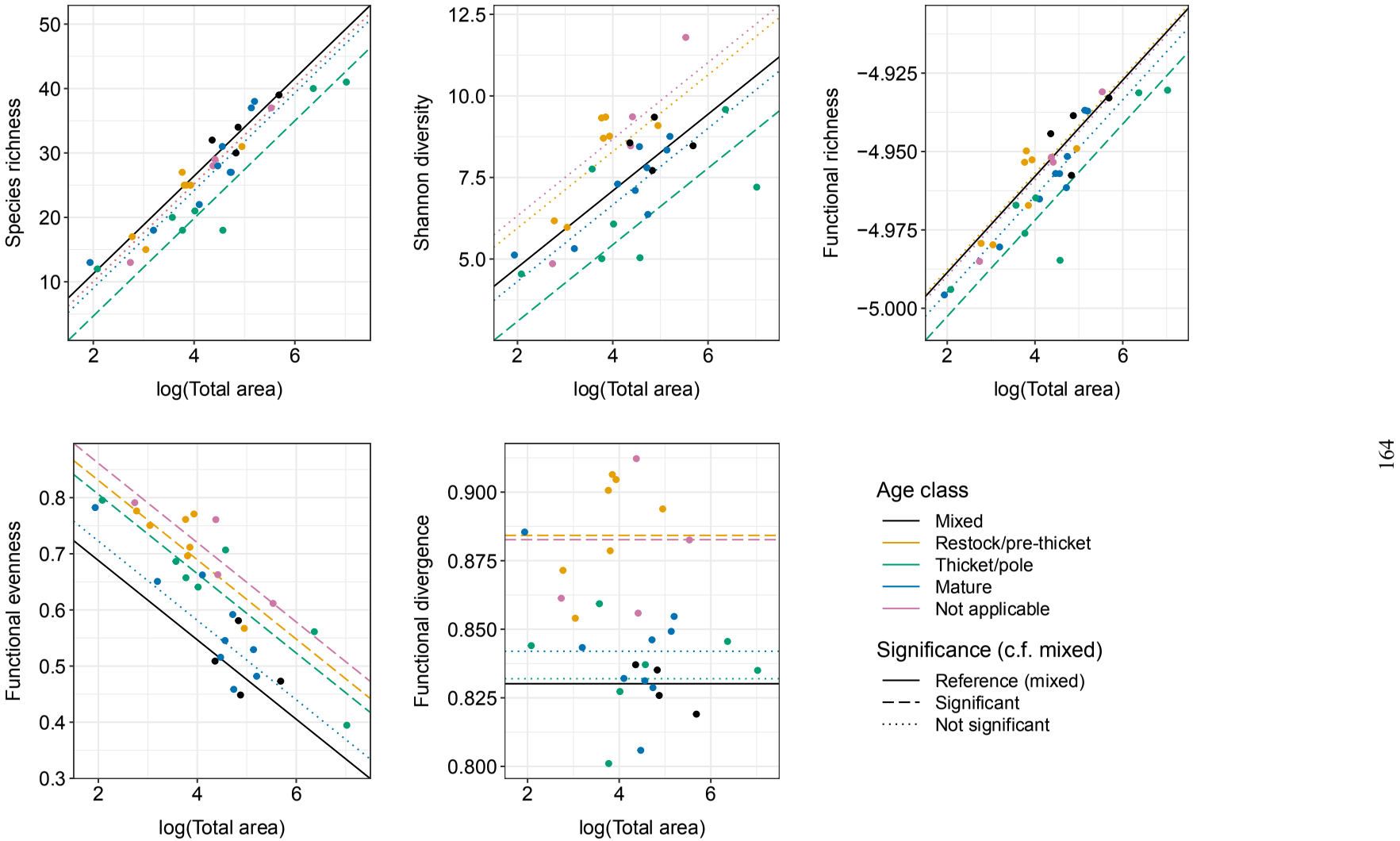

Figure 7.7: Significant linear relationships between (log) total area and diversity metrics. Colours indicate the differences between age classes. Line type shows whether the age class is significantly different to the reference mixed age class.

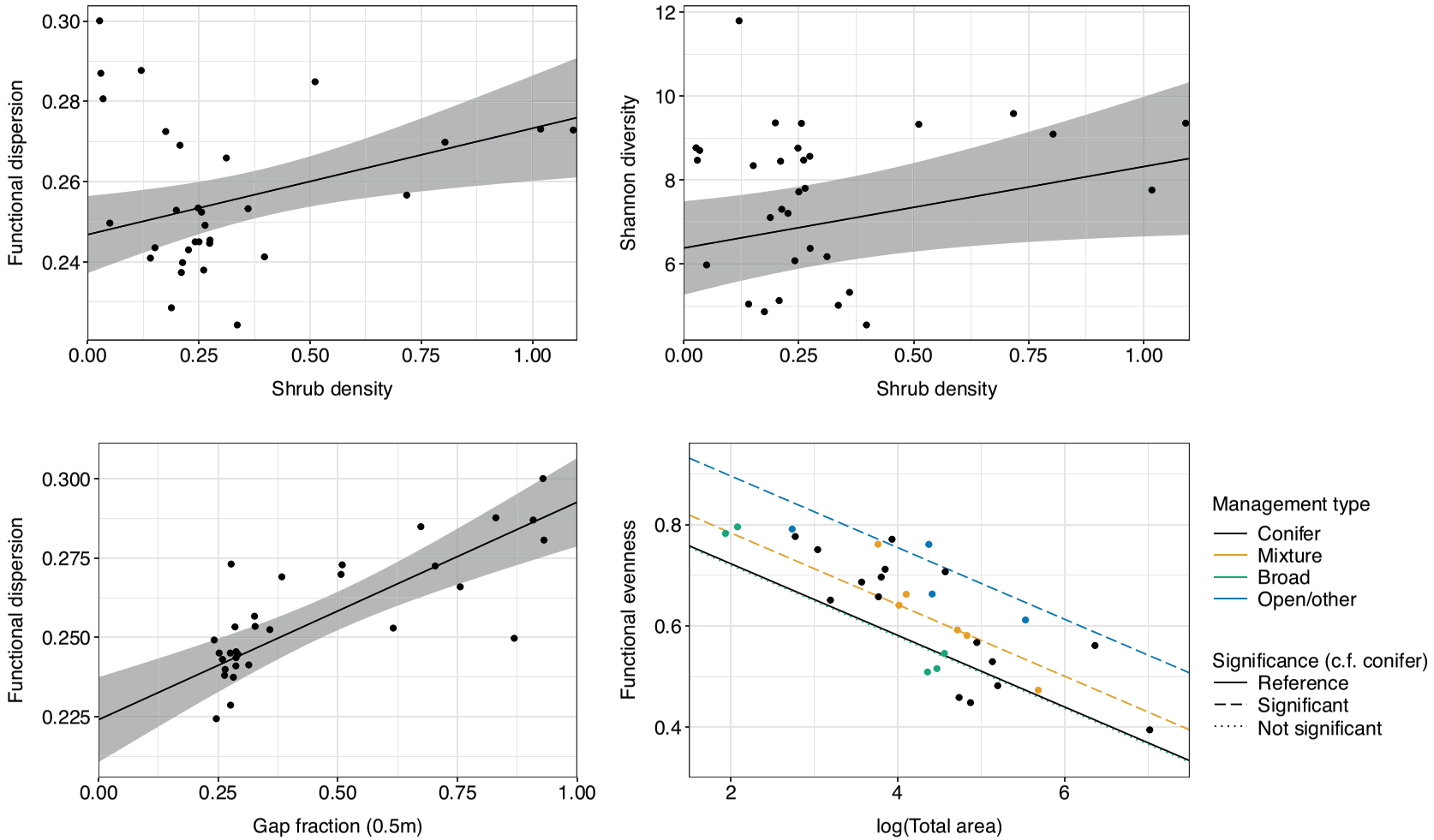

Figure 7.8: Significant linear relationships between independent variables and diversity metrics. In the top panels and the bottom left panel, the black line indicates the regression line and the grey shading indicates the 95% confidence interval. The bottom right panel shows relationship between (log) total area and functional evenness and also indicates the differences between management types and whether management variables are significant compared to the reference conifer management type (see legend).

Table 7.2: ANOVA results of the final linear models for each diversity metric. Bolding indicates significant P value. The age class 'not applicable' and management type 'open/other' categories are equivalent, so they have identical estimates (indicated by square brackets), but cannot be included in the same model (depending on variable order one category is discarded).

	Species richness			**Shannon diversity**			**Functional richness**		
	Estimate	**SE**	***P* value**	**Estimate**	**SE**	***P* value**	**Estimate**	**SE**	***P* value**
Intercept	-2.30	4.00	0.57	1.50	1.60	0.34	-5.00	0.01	**3.3e-42 (***)**
Total area (log)	7.60	0.57	**9.9e-12 (***)**	1.20	0.22	**3.4e-05 (***)**	0.02	0.00	**3e-08 (***)**
Horizontal heterogeneity (10m)	-12.00	14.00	0.40	1.10	5.50	0.85	0.02	0.04	0.67
Age class			**0.0035 (**)**			**0.0015 (**)**			**0.026 (*)**
- Mixed ages	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
- Restock/pre-thicket	-1.20	2.10	0.57	1.20	0.83	0.16	0.0009	0.0067	0.89
- Thicket/pole	-6.60	1.90	**0.0024 (**)**	-1.7	0.75	**0.039 (*)**	-0.014	0.006	**0.031 (*)**
- Mature	-2.30	1.80	0.21	-0.43	0.69	0.54	-0.0063	0.0056	0.27
- Not applicable	[-1.20]	[2.30]	[0.59]	[1.60]	[0.90]	[0.093]	[-0.0011]	[0.0072]	[0.88]
Management type			0.12			0.37			0.67
- Conifer	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
- Mixture	-0.26	1.50	0.86	0.31	0.58	0.60	-0.0022	0.0047	0.65
- Broadleaved	3.40	1.70	0.06	0.99	0.68	0.16	0.0032	0.0055	0.57
- Open/other	[-1.20]	[2.30]	[0.59]	[1.60]	[0.90]	[0.093]	[-0.0011]	[0.0072]	[0.88]
Shrub density	3.70	2.30	0.13	1.90	0.91	**0.044 (*)**	1.5e-4	0.0073	0.98

Table 7.2 continued: ANOVA results of the final linear models for each diversity metric. Bolding indicates significant P value. The age class 'not applicable' and management type 'open/other' categories are equivalent, so they have identical estimates (indicated by square brackets), but cannot be included in the same model (depending on variable order one category is discarded).

	Functional divergence			**Functional evenness**			**Functional dispersion**		
	Estimate	**SE**	***P* value**	**Estimate**	**SE**	***P* value**	**Estimate**	**SE**	***P* value**
Intercept	0.83	0.03	**3.5e-18 (***)**	0.89	0.07	**8.9e-12 (***)**	0.21	0.02	**4.7e-12 (***)**
Total area (log)	8.5e-4	0.0042	0.84	-0.071	0.0095	**2.7e-07 (***)**	6.6e-4	0.0023	0.78
Horizontal heterogeneity (10m)	-0.077	0.1	0.47	-0.28	0.23	0.24	-0.0019	0.06	0.97
Age class			**0.0015 (**)**			**7.7e-4 (***)**			
- Mixed ages	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*			
- Restock/pre-thicket	0.05	0.02	**0.0024 (**)**	0.14	0.035	**5.9e-4 (***)**			
- Thicket/pole	0.0018	0.01	0.90	0.12	0.032	**0.0014 (**)**			
- Mature	0.01	0.01	0.37	0.035	0.029	0.25			
- Not applicable	[0.053]	[0.017]	**[0.0055 (*)]**	[0.17]	[0.038]	**[1.8e-4 (***)]**			
Management type			0.92			**0.049 (*)**			0.88
- Conifer	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
- Mixture	0.003	0.01	0.79	0.061	0.025	**0.023 (*)**	0.0042	0.0059	0.49
- Broadleaved	0.0047	0.01	0.72	-0.0032	0.029	0.91	0.0009	0.0069	0.90
- Open/other	[0.053]	[0.017]	**[0.0055 (*)]**	[0.17]	[0.038]	**[1.8e-4 (***)]**	0.0033	0.0072	0.66
Shrub density	0.03	0.017	0.091	-0.0023	0.039	0.95	0.026	0.0093	**0.0092 (*)**
Gap fraction (top third) (0.5m)							0.069	0.012	**6.6e-06 (***)**

Trait-environment data

RLQ analysis and fourth-corner

For grouped data, RLQ analysis showed a significant association between traits and environment (simulated sites: $P = 2x10^{-5}$; simulated species: $P = 0.042$; $P_{max} = 0.042$). Fourth-corner analysis revealed 13 significant pairwise trait-environment associations (Figure 7.9). However, adjustment of the *P* values using the Benjamini-Hochberg correction factor removed the presence of any significant pairwise associations. Similarly, for individual subcompartment abundance data, there was a significant association between traits and environment according to RLQ analysis (simulated sites: $P = 2x10^{-5}$; simulated species: $P = 0.027$; $P_{max} = 0.027$). There were 15 significant pairwise trait-environment associations revealed by fourth-corner analysis, of which 8 were identical to the unadjusted grouped data significant associations (Figure 7.9). However, again, adjustment of the *P* values removed all significant pairwise associations.

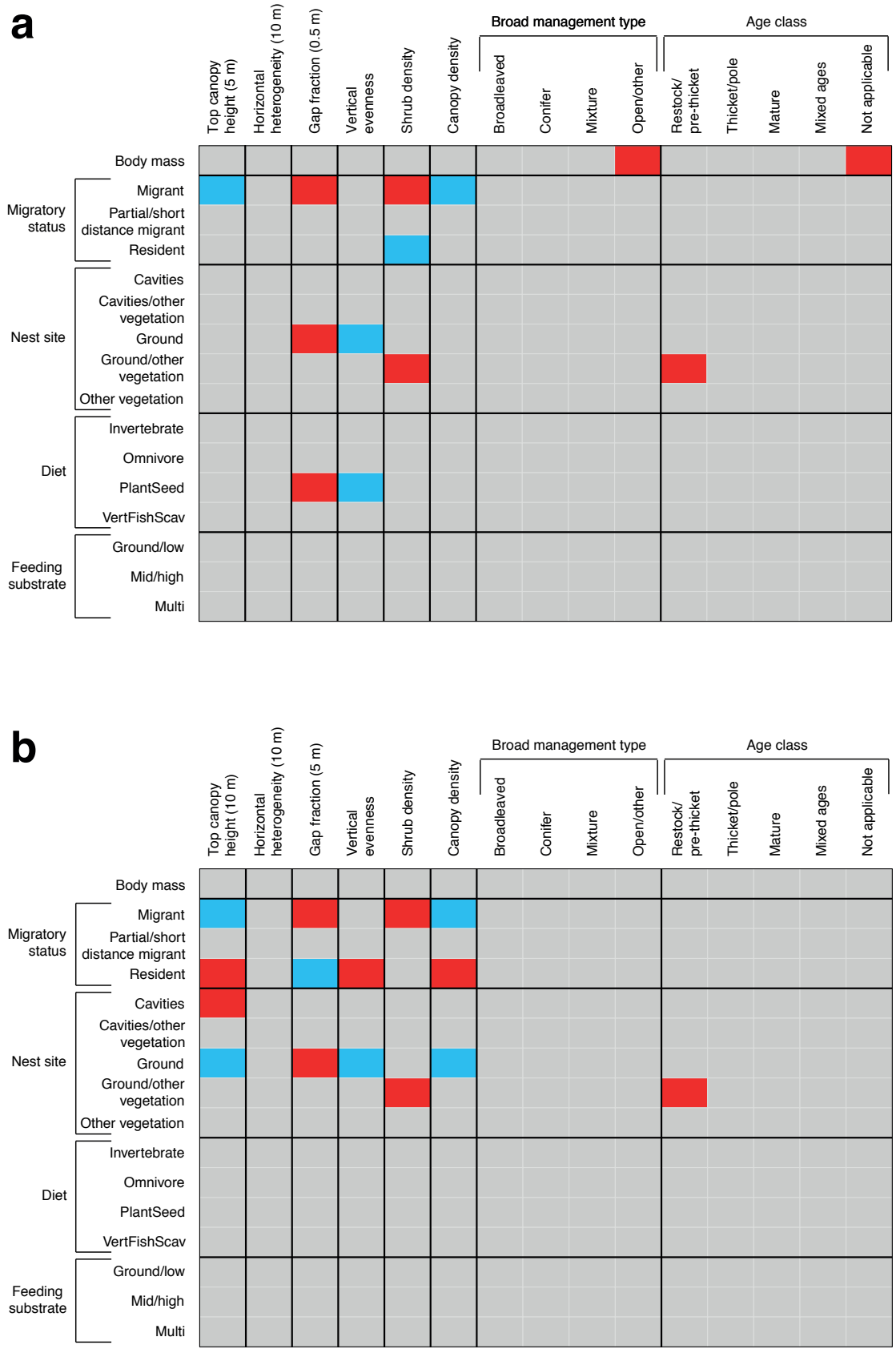

Figure 7.9: Fourth-corner analysis of a) grouped data, b) individual subcompartment data. Blue cells indicate negative significant relationships, red cells indicate positive significant relationships before adjustment of the P values using the Benjamini-Hochberg correction factor.

DISCUSSION

Structural characteristics derived from the LiDAR varied according to the resolution at which they were aggregated (Figure 7.1). In particular, gap fraction and horizontal heterogeneity decreased as they were aggregated over larger resolutions. Clearly, detail is lost as resolutions become larger, which creates a more uniform structure. From the hierarchical partitioning analysis, resolutions were ranked differently for different variables and data, demonstrating the importance of considering different resolutions for data analysis (Figure 7.2 and Figure 7.5). The largest-scale resolution was generally the best for the individual subcompartment data (with the exception of gap fraction for up to 10 m). In contrast, for the grouped data the best ranked resolutions were 5 m for top canopy height and 0.5 m for gap fraction. However, there was high variation in the percentage of independent effects and the ranks. This is expected, particularly for the individual subcompartment data, because habitat adaptations are species-specific and therefore the resolution of structural data that best explains species distributions will also be variable [353].

The most striking distinction between resolutions was for horizontal heterogeneity, where larger resolutions ranked sequentially more highly (with the exception of the 0.5 m resolution for the grouped data) and variation was relatively low. This is probably because the smaller resolutions were able to pick up the spacing distributions of the trees. However, larger resolutions distinguished more about habitat heterogeneity at a coarser scale, which appears to have been more meaningful for the majority of birds. Airborne laser scanning is increasingly being used to quantify habitat structures and their relationship to biodiversity [394], and in particular many such studies explore the effects of forest structure on bird populations (e.g. [395–401]). The results from this study suggest that the use of remote sensing data could be greatly improved if different resolutions and aggregations are first explored to determine the scale that best suits the data analysis or has the greatest predictive power.

For the species models at the level of individual subcompartments, the area variables contributed the greatest independent effects and were consistently ranked the highest across all species (Figure 7.3). This is expected, as likelihood of occupancy and detection in suitable habitat obviously increases with area. All other habitat and structural variables had relatively low independent effects percentages, and the joint and independent effects were similar, indicating that no variable was more important than others [374]. Furthermore, all variables explained very little of the total variation, with every variable except the area terms contributing less than 0.01 of the total R^2. In this context, structural and habitat attributes performed very poorly in predicting species presence or absence.

This weak explanatory power is somewhat surprising, given that so many studies find links between forest attributes and bird populations [338,345,348]. However, most studies focus on either abundance or

species richness (e.g. [333,402–405]). At the level of individual subcompartments I used occurrence rather than abundance, because subcompartments were small and so abundances were low and there was high zero inflation. It is possible that a presence/absence metric was not a sensitive enough discriminator of habitat quality, particularly given that there was low variation in some structural attributes such as vertical evenness and shrub density (Figure 7.1). Furthermore, the relatively small sizes of the stands in combination with bird mobility means that detection of bird species in a subcompartment does not necessarily reflect meaningful habitat associations. Nevertheless, the results were based on an extensive dataset involving a large number of bird observations and high-resolution habitat quality data over contiguous areas, so it is notable that habitat attributes explained so little variation. It seems likely that using the scale of forest subcompartments was insufficient to capture broader habitat information of importance, such as wider landscape heterogeneity, particularly in a large continuous forest environment. Given that many studies take place at the scale of forest stands, for practical and ecological reasons, this is an important conclusion [338,353].

It is interesting that the ranked order of variable importance changed once birds were grouped by either conservation or migratory status. This has implications for management objectives that may be targeted at either group. Top canopy height became the most important variable (other than area) for red- and amber-listed birds (Figure 7.4). This is probably because a greater proportion of the red- and amber-listed birds in this study were open habitat specialists. 82% of red- and 67% of amber-listed birds recorded in this study were classified as ground or low vegetation foragers, compared with 52% of green-listed birds (Appendix table F.1). Additionally, just 3% of green-listed birds were ground nesting, compared to 27% of red- and 17% of amber-listed birds. A low mean top canopy height would indicate that a subcompartment is relatively open, so clearly top canopy height is a key variable in determining habitat suitability for open specialists. There was a similar pattern comparing migratory and resident species. 42% of migratory birds were classified as ground or ground/other vegetation nesting, compared to 14% of resident birds. In contrast, 31% of resident birds but no migratory birds were cavity nesters. This may explain why gap fraction became a more important variable for migratory species, again as an indicator of open habitat. It is less clear why horizontal heterogeneity became relatively unimportant for both migratory species or red-/amber-listed species, although this could imply that within-stand heterogeneity was more important for forest specialists than open habitat specialists. However, as for the overall results discussed above, the percentage of independent effects for all variables except area were relatively low and their means were similar. It is therefore not possible to conclude too much from this analysis, although the results do suggest some potentially interesting trends.

Biodiversity can be measured in multiple ways, capturing separate elements of community assemblage and responding to changes in different ways [406]. Species richness is the simplest metric and so far has received the most attention in relating forest management to biodiversity [359].

However, it is increasingly recognised that other metrics may show different responses to management, and thus it is valuable to explore multiple measures [326,401,406]. Shannon diversity is another widely used metric, incorporating both species richness and abundance into a single measure. In addition to taxonomic metrics, functional diversity metrics have been identified as being particularly useful additions, especially for understanding ecosystem stability and informing conservation strategies [359,361,362]. Functional diversity is commonly represented by three independent metrics that capture different aspects of functional diversity: functional richness (the volume of functional space occupied by the community), functional evenness (the regularity of abundances within the functional space) and functional divergence (the distribution of abundances within the functional space) [407–410]. In addition, functional dispersion was proposed by Laliberté and Legendre (2010) [390] as a way of combining the distribution of species in functional space with abundance; it is the mean distance of species to the centroid value in the functional space, weighted by species abundance. Overall, the nine habitat variables used in this study explained between 76% and 94% of total variation for the different diversity metrics. Individual habitat variables explained very different levels of variation and were ranked in different orders of importance for each diversity metric. Furthermore, in the final linear models, different combinations of habitat variables were significant predictors for the different diversity metrics. These results add further evidence that management affects different components of biodiversity in contrasting ways, not just at the level of species but also the ways in which diversity is quantified, and emphasises the importance of considering multiple metrics [326,406].

The total area variable explained a large proportion of the variance for both species richness and functional richness (Figure 7.6), as expected given the classic species-area relationship [407,411]. However, it was the age class variable that was consistently important for each of the six diversity metrics, ranking either first or second out of all variables and attributed between 0.10 and 0.16 of the total variation. It was also a significant predictor in all the linear models in which it was included (species richness, Shannon diversity, functional richness, functional evenness, functional divergence). Stand age is widely found to be a fundamental variable affecting forest bird assemblages and diversity [329,345,412,413]. In particular, the early and late successional stages tend to have the highest diversity, with fewer species associated with intermediate stages (which is the most widespread age class in most rotational clearfell forestry systems) [329,332,345]. The results from this study support this general observation, as the thicket/pole age class (the intermediate stage) had relatively low diversity. For species richness, Shannon diversity and functional richness, all age classes were significantly no different to the mixed age class, except the thicket/pole age class, which had significantly lower diversity (Figure 7.7 and Table 7.2). Furthermore, the restock/pre-thicket age class and not applicable class (indicating open rather than forestry stands) had significantly higher functional evenness and functional divergence than the reference mixed class,

whereas the mature age class was no different. The one exception for the thicket/pole age class was for functional evenness, when it joined the early successional stages in having significantly higher evenness than the reference mixed class. These results clearly demonstrate the importance of age class for bird diversity, particularly the early successional stages. To maximise total diversity across the landscape, it will be necessary to ensure that there is a varied matrix of age classes. This is an unsurprising but informative result for forest managers. A potential limitation to the uptake of conservation objectives into forest management is confusion over terminology and difficulties in interpreting the implications of ecological results in terms of practical forestry [329]. To address this, these age classes were deliberately chosen as they are the categorisations widely used in forest planning. These results are therefore particularly meaningful in an applied context.

Many forest bird species show a preference for conifer or broadleaved trees, although habitat associations vary regionally [338,414]. Broadleaved forests generally tend to have higher abundance and species richness than conifer forests, but this is variable [338,415]. Interestingly, mixed forests often hold the greatest diversity because they can support both conifer and broadleaved specialists [329,345,416]. In this study, the broad management type was only a significant predictor for functional evenness. Broadleaved habitat was no different to conifer, but mixtures and open/other habitat had significantly higher functional evenness than conifers (Figure 7.8 and Table 7.2). This supports the notion that mixtures can promote diversity beyond pure conifer or broadleaved stands, but in a limited way. As found elsewhere, more basic measures of diversity such as species richness were not affected by management type [415–417].

Shrub density was a significantly positive predictor of both Shannon diversity and functional dispersion (Figure 7.8 and Table 7.2). This is particularly noteworthy given that there was relatively little overall variation in shrub density across the forest (Figure 7.1). Various birds associated with the shrub layer can be supported both by early successional stages in clearfell systems and by a shrub understorey in continuous-cover systems [403]. However, in UK woodlands, high wild deer populations cause intense browsing pressure, with resultant impacts on shrub density and well-known effects on bird populations [87,329,418]. It is therefore difficult to increase shrub density levels without large-scale and expensive interventions, such as fencing. These results emphasise the importance of even subtle variations in shrub density for bird diversity, particularly in comparison to other structural attributes of stands. Nevertheless, given that the significant relationships between shrub density and both Shannon diversity and functional dispersion were only weakly positive, and the difficulties in increasing shrub density attributes due to external factors, this may not be the best opportunity for increasing overall bird diversity within the forest.

The creation of small gaps, either through management or naturally, has been shown to increase bird diversity and abundance [405,419]. In this study, gap fraction was a significant and strongly positive predictor of functional dispersion, but not the other diversity metrics. Continuous-cover forestry

systems – where trees are harvested singularly or in small patches rather than at the stand-level as in rotational clearfell – create greater structural complexity and heterogeneity at the small scale. They are much closer in structure to a natural forest than even-aged, clearfell management systems. However, in comparing continuous-cover to clearfell systems, results for bird diversity overall are mixed and certain groups of birds are found to favour different management types [329,403,420,421]. I did not measure continuous-cover as a type of management directly in this study, but would expect the subcompartment horizontal heterogeneity, vertical evenness and gap fraction to increase as a result of continuous-cover management. Notably, vertical evenness was consistently ranked lowly in the hierarchical partitioning across all diversity metrics and was not included in the final models, and while horizontal heterogeneity was ranked more highly overall in the hierarchical partitioning, it was not significantly associated with any diversity metric. As discussed, gap fraction was significantly positively related to functional dispersion only. It is possible that a lack of variation between stands meant that effects could not be detected, but these results suggest that birds are not responding strongly to structural variation within the stand.

It is often assumed that increasing within-stand diversity will benefit biodiversity, although evidence for this is mixed and largely lacking [422–424]. Interestingly, a number of recent studies have concluded that increasing wider landscape heterogeneity is essential to maximise biodiversity in managed forests, whereas focusing on increasing within-stand heterogeneity has limited benefits if the wider landscape is homogenous [326,340,423]. In this study, the main habitat attribute influencing diversity metrics was age class, with both early and late successional stages being important. Creating a landscape matrix that consists of a variety, and provides a continuity, of age classes will thus be of crucial importance for bird diversity. Therefore, although I did not measure the effects of the wider landscape directly in this study, the results seem to add evidence to the emerging trend that between-stand, rather than within-stand, heterogeneity is of fundamental importance.

The fourth-corner analysis showed that there was a significant relationship between species and environmental traits. However, following adjustment of the *P* values through a correction factor, no individual pairwise trait-environment association remained significant. This suggests that there were important interactions between species traits and the habitat variables, as would be predicted given basic evolutionary principles [365], but the separate pairwise interactions were not strong enough to be detected statistically with this dataset. It seems likely that this is at least partly because the birds were not isolated in the sites where they were recorded; Thetford Forest is an extensive, largely continuous forest, the individual subcompartments are relatively small and the birds mobile. Most birds are therefore able to easily move to find resources, and so trait-environment associations based on static sampling at the subcompartment scale will be difficult to detect.

Broad age classes were found to be generally more important in the diversity models but, intriguingly, it was the structural data that had the most significant pairwise trait-environment

interactions before adjustment with the correction factor (Figure 7.9). This indicates that within-stand structural attributes are more important for individual species specialisations, particularly for a subset of traits like migratory status, whereas broader-scale heterogeneity is essential to maximise diversity more generally. However, to explore these individual species-trait associations in more detail, alternative sampling techniques would be necessary, such as by finding the total time spent by individuals in different habitats.

There is a growing body of literature exploring the relationship between forest attributes and bird diversity. In general, forest structural complexity and diversity is deemed to be critical for biodiversity conservation [329,331,348,353]. However, it is striking how inconsistently different variables are found to be important, across different regions, forest types, taxa and diversity metrics. This study has emphasised the importance of certain variables, such as age class, but not found relationships with commonly important variables such as canopy density, vertical heterogeneity and horizontal heterogeneity [394,401]. There were a range of limitations; for example, I did not consider the distance to forest edge or recreation impacts [329,425]. Nevertheless, the key factor affecting the results of this study appears to be using the scale of a forest subcompartment. This has particular advantages for informing practical forest management, as this is the scale at which management decisions are taken. However, the spatial grain used will change the order of importance of different environmental variables [401,426]. The results of this study indicate that it is overall landscape heterogeneity, rather than increasing within-stand heterogeneity, that will maximise bird diversity within the managed forest landscape. Given that this appears to be an emerging trend in managed forest research, it would be valuable for future research to explore this further.

8 | Bringing it all together: synergies, trade-offs and the optimal landscape

SUMMARY

There is relatively little incorporation of the ecosystem services framework into practical land management and planning, despite it being a highly active academic research area. Key areas where research needs to be improved to increase its uptake in applied situations include the involvement of stakeholders in order to ensure researchers use realistic scenarios, the analysis of relationships between a wide range of ecosystem services, and the production of specific and comprehensible management recommendations. In this final chapter, I illustrate how these issues can be addressed by bringing together the analyses of previous chapters to quantify the relationships between 11 ecosystem services delivered from 36 different management options in Thetford Forest. I establish which options are the most efficient in terms of ecosystem service delivery and use multi-criteria decision analysis to generate recommendations for landscape configurations that achieve maximum ecosystem service delivery. I also explore how different values and perspectives affect such recommendations. By evaluating the top proportion of the best-performing landscape configurations, I found that recommendations were remarkably consistent, regardless of the weightings or utility functions that were applied. Both open space and conifer monocultures were a crucial component of the 'ideal landscape', together being roughly 65% of the total area; the remainder was split between mixtures and broadleaves. This recommendation also aligns with the results from the chapter on biodiversity, which found that a wide-scale diversity of stands, including an open space component, was important. The results from this chapter are of direct practical application for the future management of Thetford Forest, but the analysis also represents a case study of research that applies the ecosystem services framework to generate meaningful recommendations for decision makers and land managers.

INTRODUCTION

Ecosystem services research has grown greatly over recent years [18,19,427]. Despite this enthusiasm, there is limited practical application of the concept, and its integration into management and planning remains a major challenge [26,42,428]. Key research issues include the consideration of a comprehensive suite of ecosystem services (rather than a few, easily quantifiable services), relationships between them in complex environments, and the engagement of stakeholders to ensure that research is grounded in realistic scenarios [36,39]. It is also important for research to recognise

that ecosystem services are co-produced by both humans and the natural environment, i.e. humans influence the ecological processes that give rise to goods and benefits through land modification and management [13,34,268]. Finally, although the field is undeniably complex, decision-makers need specific recommendations to incorporate the ecosystem services framework into planning decisions, yet relatively few studies provide such recommendations [34].

Forests can deliver an extensive variety of ecosystem services, such as timber production, carbon sequestration, recreation and heritage values [12,46,282,429]. Their management, which affects the structure and functioning of the forest, is fundamental to ecosystem service delivery [430]. Traditionally many forests have been managed to maximise only one or a few services, notably timber production [431,432]. However, the importance and benefits of providing a wide range of ecosystem services from forests is widely recognised, and aligns with established multi-functional and sustainable forest management strategies [433,434]. They thus provide an excellent case study for examining how the quantification of ecosystem services can influence policy making and practice.

Management has varying effects on different ecosystem services, leading to trade-offs and synergies [42,435]. Trade-offs are recorded more often than synergies, although the majority of studies concerning ecosystem services do not analyse trade-offs at all, and even fewer consider synergies [34,42,274,323]. Generally, no particular type of forest attribute or management option is able to simultaneously maximise all ecosystem services [46,282,430]. Therefore, when the production of multiple benefits is the objective, it is challenging for forest managers to devise a suitable management strategy [436].

There is relatively little understanding of how forest management affects ecosystem service delivery and how it can be used to reconcile trade-offs [54,282]. To effectively inform, and translate into land management decisions, research needs to be conducted at a scale that is relevant; this includes focusing on the physical scale of the management unit and the scale of realistic management alternatives. Studies often focus on fairly coarse differences between management options (such as between broad habitat types, like forest versus agricultural land), whereas in reality decision-makers are often concerned with much finer differences (such as the species composition of a forest management unit). It is therefore important to engage stakeholders, to ensure that research is targeted and to encourage consideration and incorporation of the results, yet stakeholders are rarely involved in ecosystem services studies [34,42].

Trade-offs and synergies between ecosystem services can be balanced through economic evaluations, such as cost-benefit analysis [42,433]. However, monetary valuation techniques are controversial and multi-criteria decision analysis is now generally considered to be more appropriate for ecosystem service assessments, being better able to deal with a range of perspectives and integrate varying types of data, methods and information [42,433,437]. Multi-criteria decision

analysis is already widely used in research relating to forest management and planning, and environmental planning and decision-making more broadly; it is also now increasingly used for ecosystem service assessments [437–441].

In addition to ecological values, social and economic values are important dimensions of ecosystem service assessments [38,438,442]. Multi-criteria decision analysis is particularly useful due to its flexibility in incorporating information about preferences and values. The importance of different ecosystem services, which can depend on the social context or be driven by economic considerations, can be included by altering the weights of the attributes (which in this case are the ecosystem services) in the multi-criteria decision analysis [436,443]. Additionally, utility functions are used to transform the performance of an attribute into a measure of value or utility [444,445]. Often, studies assume a simple linear increasing or decreasing relationship between attribute performance and value, but this is normally an oversimplification [446]. In reality, utility functions will usually be non-linear, reflecting differences in marginal value at different levels of ecosystem service delivery [444]. Both attribute weights and utility functions can greatly change the outcomes of multi-criteria decision analysis, and are therefore important considerations [436,447]. For this reason, sensitivity analysis is a crucial component of such assessments [445]. Furthermore, the supply and demand for different ecosystem services will change in future, so it is informative to understand how outcomes are affected by such changes, particularly in an industry such as forestry where the consequences of land management decisions take place over long timescales [34,433,448].

Here, I address these research gaps and recommendations to generate evidence that is of direct practical application. For a UK forest landscape, I analyse the trade-offs and synergies between the delivery of a comprehensive suite of ecosystem services from a range of realistic management alternatives. These capture the breadth and detail of management options that are under consideration for the future of the forest. In particular, I make recommendations for the landscape composition that can maximise overall ecosystem service value, and explore how this is affected when weightings and utility functions are altered. The aim is to generate results that are informative and understandable for forest managers, promoting the use of the ecosystem services framework in practical decision making.

METHODS

Ecosystem service values were gathered for 36 management options, which represent the full range of scenarios under consideration for the future management of Thetford Forest (Appendix table G.1). The Forestry Commission was engaged extensively at the start of the research project to identify which management options are both feasible and acceptable in the forest. I included 11

ecosystem service measures: timber, carbon†, water, deer, soil quality (total carbon), soil quality (total nitrogen), soil quality (C:N ratio), wildlife, recreation, scenic beauty and heritage. Each ecosystem service value was generated through detailed analysis specifically targeted to the Thetford Forest landscape (see chapters 2-6), rather than relying on look-up tables or secondary data, as is often the case when studying multiple ecosystem services [34]. Where values were not calculated specifically for an individual management option, due to unavailability of data, I used the closest alternative; for example, for western hemlock monoculture, the 'other conifer monoculture' category was used for deer and cultural services (Appendix table G.2). I was unable to calculate water supply values directly for eucalyptus due to lack of data, but it is known to have high water use [449]. Assigning eucalyptus the water use value of other broadleaves would therefore be inappropriate, and given that it is unlikely to be a large component of any future landscape, I excluded it from the analysis for the next stage.

To determine which ecosystem services were in synergy or in conflict, I created linear models using the data from all the 36 management options for all unique pairwise comparisons of ecosystem services and calculated the Pearson correlation coefficient for each. To account for multiple testing on the same data, I calculated the Benjamini-Hochberg correction factor using a false discovery rate of 5%, which gave a corrected *P* value of 0.0033.

For the multi-criteria decision analysis, I then scaled values for each ecosystem service so that they were comparable to one another. I used a maximising function for all ecosystem services where a larger value is preferable to a smaller value:

$$\tilde{x} = \frac{x - \min_x}{\max_x - \min_x}$$

where,

$\tilde{x}$ = the scaled value

x = the raw ecosystem service value,

$\max_x$ = the maximum value of all the raw ecosystem service values,

$\min_x$ = the minimum value of all the raw ecosystem service values.

This scales values between 0 and |1| such that the smallest value is 0 and the largest value is 1 for positive scales (Figure 8.1a). For deer, which was on a negative cost scale, the smallest value was -1 and the largest value was 0 (Figure 8.1b). The raw values for water supply were over both a positive and a negative scale. I therefore assigned $\min_x = 0$, which scaled values relative to $\max_x$ but kept values on their respective positive or negative axis (Figure 8.1c).

† The above-ground carbon storage potential of trees.

For the C:N ratio indicator of soil quality, smaller values are preferable to larger values, so I used a minimising function (Figure 8.1d):

$$\tilde{x} = \frac{\max_x - x}{\max_x - \min_x}$$

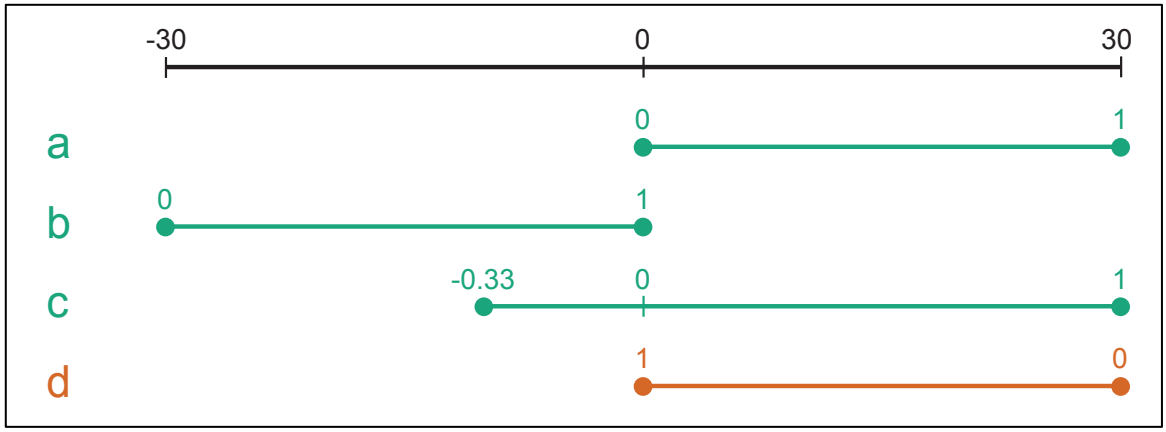

Figure 8.1: The different scaling functions used. The black line and values indicate raw values. Green lines indicate maximising functions, the orange line indicates a minimising function. Circles represent the minimum and maximum limits for each line. (a) A maximising function used to scale values on a positive axis. (b) A maximising function used to scale values on a negative axis. (c) A maximising function used to scale values that span both a positive and negative axis. (d) A minimising function used to scale values on a positive axis.

I then reduced the number of management options under consideration by retaining only the options that had Pareto efficiency, i.e. where it was not possible to improve on one ecosystem service without leading to a compromise on another by choosing an alternative management option.

I used multi-attribute utility analysis, which is a form of simple additive weighting that also applies utility functions. The scaled values of each attribute (ecosystem service) were multiplied by a utility function[‡], which captures the relationship between increasing the attribute and the utility gained, which may not be linear. Therefore, the total utility for each management option was calculated as follows:

$$\sum_{i=1}^{i=n} u(a_i)$$

where,

u = the utility function

[‡] For clarity of terminology I use the phrase ‘utility function’, but note that elsewhere this might be referred to as a ‘value function’.

a_i = the scaled value of the i^{th} attribute

Assuming an equal preference for all the ecosystem services, the total range for the utility values for each service was 1, i.e. the utilities of the minimum and maximum values were 0 and 1, respectively (or -1 and 0 on the negative axis). As there were three measures of soil quality, I divided the utility for each measure by three, so that the total utility contributed for soil quality was equal to the other ecosystem service attributes. For water, which had values over two axes, I divided the utility values generated from the utility function by the total range, so that they also had a range of 1. For example, if the maximum scaled value was 1 and the minimum value -0.5, a linear utility function would give utility values of 1 and -0.5, with a range of 1.5. The scaled utility values would therefore be between -1/3 and 2/3.

To explore how outputs varied according to the utility function, I repeated the analysis with a series of functions. Firstly, I used a linear function, $u(a_i) = m(a_i)$, where $m = 1$. However, marginal utility functions with diminishing returns are often a more realistic representation of the utility gained from increasing ecosystem service values, as follows:

$$u(a_i) = \frac{1 - \exp\left[\frac{-(a_i - \min_a)}{\rho}\right]}{1 - \exp\left[\frac{-(\max_a - \min_a)}{\rho}\right]}$$

For $0 \leq a_i \leq 1, \min_a = 0, \max_a = 1, \rho = \rho_{pos}$

For $-1 \leq a_i < 0, \min_a = -1, \max_a = 0, \rho = \rho_{pos} \times -1$

I used five different ρ coefficient values – |0.1|, |0.25|, |0.35|, |0.6|, |1.2| – which were the coefficients (within 0.05) that most closely approximated values of 0.6, 0.7, 0.8, 0.9 and 0.99 when a_i = 0.5. All six utility functions are illustrated in Figure 8.2.

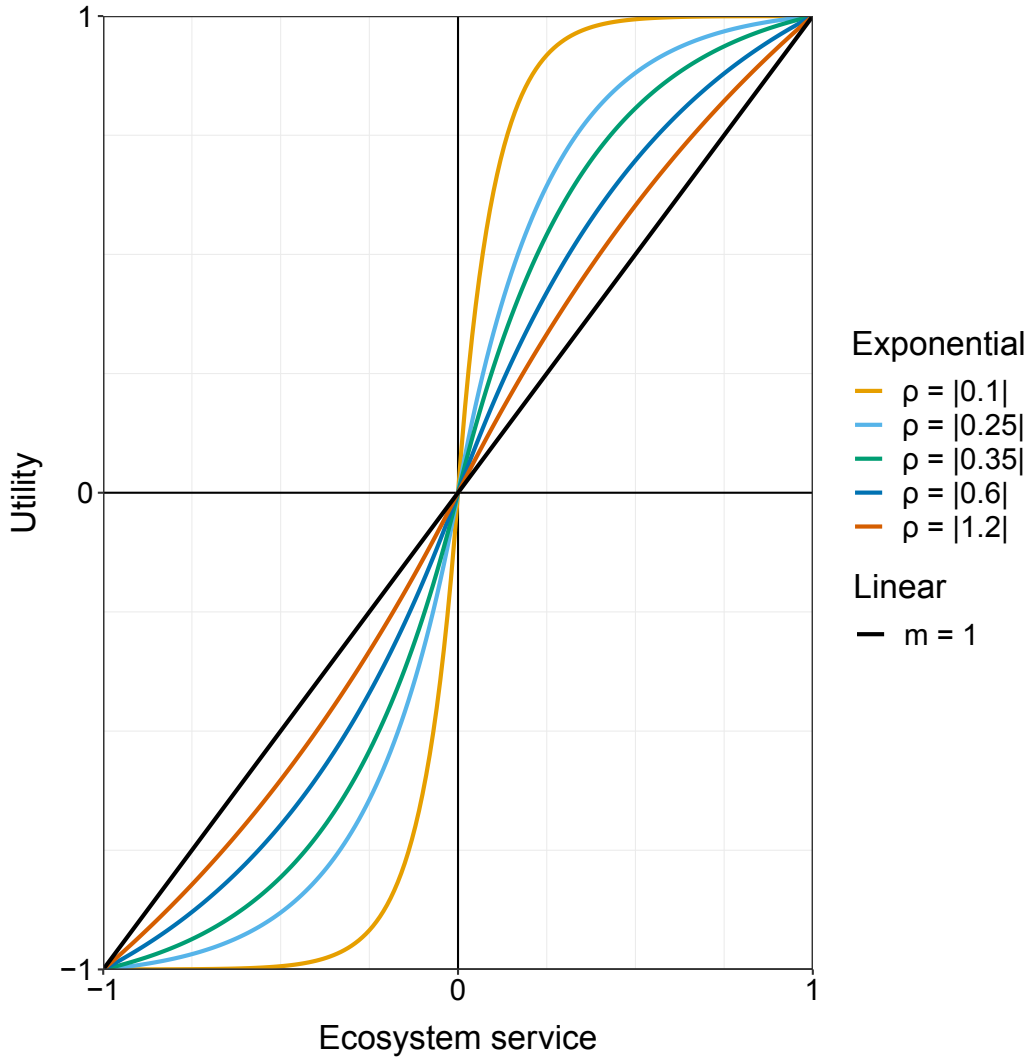

Figure 8.2: The six utility functions used in the analysis. The legend indicates the different coefficient values for each utility function.

Following the calculation of the overall 'best' management option under different utility functions, I explored the optimal landscape configuration. I divided the hypothetical landscape into ten equal blocks and assigned a management option to each block. Each management option could be assigned to between 0 and 10 blocks to each landscape; there were 352,716 unique landscape configurations. For each potential landscape configuration, I weighted the scaled attribute (ecosystem service) value of each management option by its percentage composition and applied the utility function to this weighted value for each ecosystem service. Finally, I calculated the total utility for each landscape configuration:

$$\sum_{i=1}^{i=n} u\left(a_{i,j} \times p_j + a_{i,k} \times p_k \ldots a_{i,n} \times p_n\right)$$

$$p_j + p_k \ldots + p_n = 1$$

where,

$a_{i,j}$ = the value of attribute i from management option j

p_j = the proportion of management option j in the landscape configuration

I calculated the overall maximum utility across all potential landscape configurations, which corresponds to the optimal landscape. I repeated this analysis for all the six utility functions. However, many other landscapes have very similar values to the optimal landscape but are not the strict optimum. Therefore, for the top 10% and top 5% of total landscape utility values, I calculated the mean percentage composition for each management option.

Thus far, all ecosystem service categories were assigned equal weights. I then conducted a sensitivity analysis by changing the weights of the different ecosystem services. I used an intermediate utility function (ρ = |0.45|, which most closely approximates a value of 0.75 when a_i = 0.5). For each ecosystem service I applied a weight of between 0 and 1 in 0.05 increments, which represented the weight of that ecosystem service relative to all other ecosystem services. For example, attributing a weight of 0.5 to timber would weight it the same as all the other ecosystem services combined; a weight of 0.9 would mean that all other ecosystem services were given a total weight of 0.1. For each of the 20 weighting options for each ecosystem service, I calculated the total utility for each management option, as follows:

$$w_A[u(A)] + \left\{[1 - w_A] \times \left[\sum_{i=1}^{i=n} u(a_i)\right]\right\}$$

where,

A = the target attribute (ecosystem service) that is weighted

$a_{i\ldots n}$ = all attributes except A

w_A = the weight applied to A

I calculated the rank of each management option at every weight and ecosystem service combination to track how the preferences for management options changed as weightings differed.

I then repeated the landscape configuration analysis to find the optimal landscape for each weighting. The total utility for each landscape configuration was as follows:

$$w_A\left[u\left(A_j \times p_j + A_k \times p_k \dots A_n \times p_n\right)\right] + \left\{[1 - w_A] \times \left[\sum_{i=1}^{i=n} u\left(a_{i,j} \times p_j + a_{i,k} \times p_k \dots a_{i,n} \times p_n\right)\right]\right\}$$

In reality, different ecosystem services will have different utility functions. The overall utility curve of all ecosystem services is likely to be a non-linear curve of diminishing returns: marginal utility gains decrease as more of the ecosystem service is delivered (black line in Figure 8.3a). For example, increasing ecosystem service delivery from 0 to 0.25 will give high utility gains (U1 in Figure 8.3a), as the baseline of 0 is undesirable. This could be equivalent to increasing local timber production from 0 to 1,000 tonnes, creating a benefit when previously there was none and therefore generating substantial increase in wellbeing. In contrast, further increasing ecosystem service delivery when there is already a high baseline, such as from 0.75 to 1, will have a less dramatic effect on human wellbeing and thus a smaller increase in utility (U2 in Figure 8.3a). Increasing timber production from 3,000 to 4,000 tonnes clearly has some value, but its impact is not as significant as the increase from 0 to 1,000 tonnes. However, the exact relationship between ecosystem service delivery and utility will differ for each ecosystem service, according to the scale at which they generate benefits. The benefits of some services are aggregated at the regional, national or even global scale, such as water supply, timber and carbon. When considered at the national level, the total possible increase from 0 to 4,000 tonnes of local timber represents a small fraction of the overall potential timber production across the country (blue box in Figure 8.3a). This small section of the overall utility curve corresponds to an essentially linear relationship between the ecosystem service delivery achieved at the local scale and the overall utility this generates (Figure 8.3b). In contrast, the benefits of other ecosystem services are realised almost entirely at the local scale, such as recreation and scenic beauty. The benefit that they generate cannot be compensated for by increasing recreation or scenic beauty in another part of the country. The range of ecosystem service values from the local context therefore represents the full range of utility (green outer box in Figure 8.3a), corresponding to a non-linear relationship between local ecosystem service delivery and overall utility (Figure 8.3c).

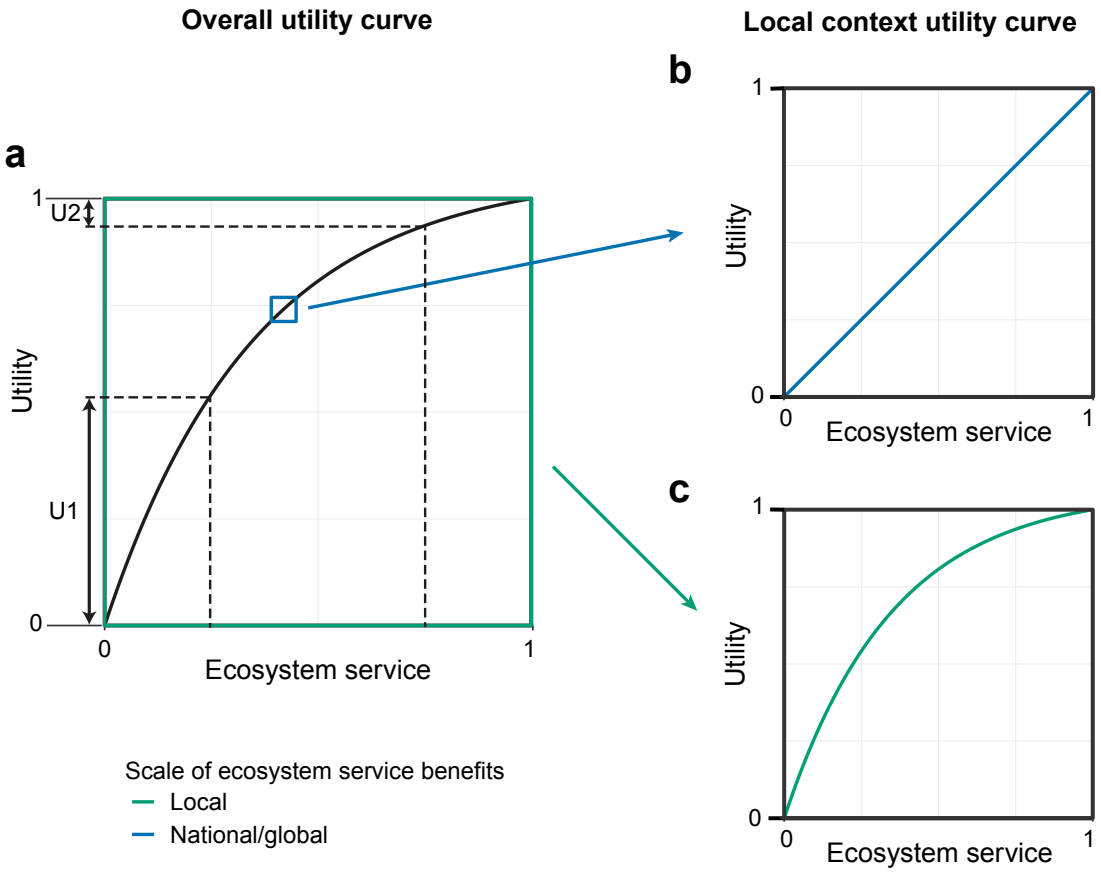

Figure 8.3: The difference in expected utility function from ecosystem services that have different scales of benefit. (a) The black curve represents the overall utility curve generated by ecosystem services. Gains in utility when ecosystem service delivery is increased by 0.25 are indicated by U1 (0 to 0.25) and U2 (0.75 to 1). The utility curve has diminishing marginal returns, therefore U1 > U2. When the scale of benefit being considered is national or global (such as national timber production), the contribution from a local landscape will represent only a small section of the overall utility curve (blue box). In contrast, when the scale of benefit being considered is only local (such as recreation), the contribution from a local landscape will represent the whole range of the overall utility curve (green box). (b) The local contribution of services that have national or global benefits. The blue box from (a) is scaled to represent the full range of ecosystem service delivery from the local level. The relationship between minimum and maximum utility at the local level is almost linear. (c) The local contribution of services that have only local benefits. The green box from (a) is scaled to represent the full range of ecosystem service delivery from the local level. The relationship between minimum and maximum utility at the local level is non-linear.

Therefore, finally, I ran the landscape optimisations with different utility functions for different ecosystem services. I set timber, carbon and water as a linear utility function (as these services are of wide-scale importance) and applied exponential functions to the other ecosystem services, running optimisations for all the coefficients. I found the optimal landscape configuration for each set of utility functions, as well as the mean percentage composition of different management options for the top 10% and 5% of landscape utility values.

RESULTS

Of the 55 unique pairwise comparisons of ecosystem services, 18 had a significant linear relationship, indicating a synergy or trade-off (Figure 8.4). Timber, carbon and the three indicators of soil quality all had 5 significant relationships with other ecosystem services. Timber, carbon and soil quality (total carbon and total nitrogen) were all in synergy with each other and in trade-off with water and soil quality (C:N). Water was negatively correlated with soil quality (C:N) and therefore in synergy (as smaller values of C:N are preferable). Deer was in synergy with both wildlife and heritage while recreation was in trade-off with scenic beauty. When ecosystem services were grouped according to convention (provisioning – timber, deer, water; regulating – carbon, soil quality; cultural – wildlife, recreation, scenic beauty, heritage), there was no general trend in the type of relationship (synergy or trade-off) between these different groups.

From the 36 original management options, 12 had Pareto efficiency (i.e. there was not an alternative management option that was universally equal to or better across all ecosystem services). These were: Douglas fir monoculture, Japanese larch monoculture, Scots pine monoculture, western hemlock monoculture, conifer mixture with a Scots pine pioneer, conifer mixture with a hybrid larch pioneer, Scots pine and beech mixture, birch monoculture, sweet chestnut monoculture, other broadleaved monoculture, broadleaved mixture without a pioneer, open space. The scaled ecosystem service delivery of these options is represented in Figure 8.5.

There were some clear trade-offs between different options. For example, open space did not deliver any timber, carbon[§] or soil quality (total carbon and total nitrogen), which all other options did deliver. However, open space delivered the highest levels of water and soil quality (C:N), was consistently high across the four cultural services (wildlife, recreation, scenic beauty, heritage) and did not deliver any negative deer ecosystem service. Differences between the forested options were often much more subtle, although the most dramatic changes were generally across the cultural services.

For all utility functions except the most extreme exponential curve ($\rho = |0.1|$), the open space option delivered the greatest overall utility (Figure 8.6). When $\rho = |0.1|$, broadleaved mixture was the best option, although this reduced dramatically in relative value and rank as the utility function became more linear. The relative value and ranks of the broadleaved monocultures also decreased with increasing linearity of the utility function. In contrast, the values of conifer monocultures, mixtures

[§] This is according to the assumptions of the analysis, which calculated above-ground carbon storage potential of trees. Some carbon will of course be stored in the vegetation of open space habitats, although this will be small compared to the forested options [94].

and the conifer and broadleaved mixture were generally consistent relative to the maximum value of the best option. They increased in rank as the utility functions were increasingly linear due to the falling value of the broadleaved options. Japanese larch was the best conifer option until $\rho = |1.2|$, when it fell below other conifer options; western hemlock was consistently the worst conifer option. Douglas fir increased in rank from being the second worst option at $\rho = |0.1|$ to the second best option when the utility function was linear. The most dramatic change in the ranks of management options was between $\rho = |0.1|$ and $\rho = |0.25|$.

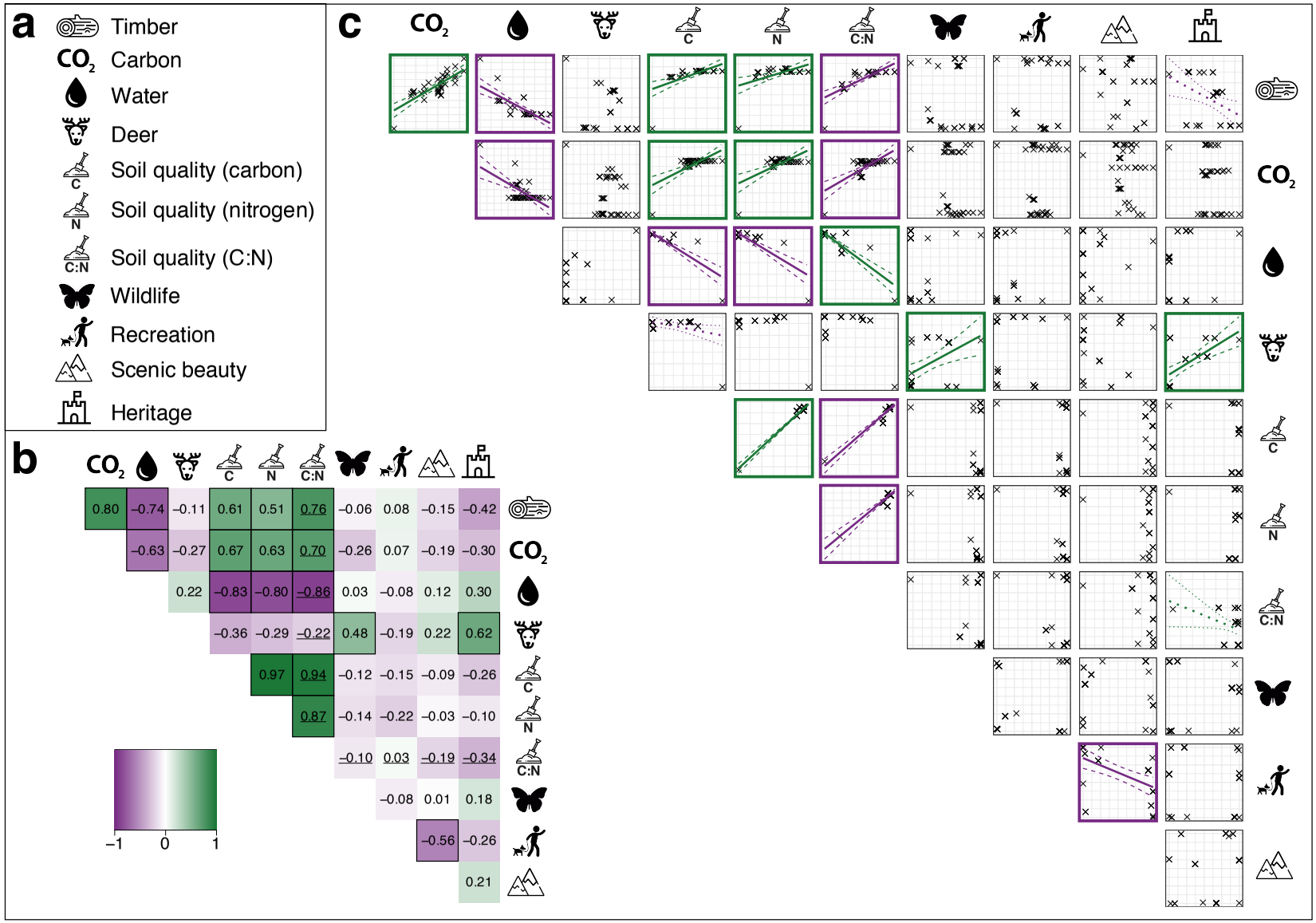
a
Timber
Carbon
Water
Deer
Soil quality (carbon)
Soil quality (nitrogen)
Soil quality (C:N)
Wildlife
Recreation
Scenic beauty
Heritage
b
0.80 −0.74 −0.11 0.61 0.51 0.76 −0.06 0.08 −0.15 −0.42
−0.63 −0.27 0.67 0.63 0.70 −0.26 0.07 −0.19 −0.30
0.22 −0.83 −0.80 −0.86 0.03 −0.08 0.12 0.30
−0.36 −0.29 −0.22 0.48 −0.19 0.22 0.62
0.97 0.94 −0.12 −0.15 −0.09 −0.26
0.87 −0.14 −0.22 −0.03 −0.10
−0.10 0.03 −0.19 −0.34
−0.08 0.01 0.18
−0.56 −0.26
0.21
−1 0 1
c
CO2
C
N
C:N

Figure 8.4: Trade-offs and synergies between ecosystem services. a) All ecosystem services included and symbology. b) Pearson correlation coefficient between pairs of ecosystem services. Note that for soil quality (C:N) (underlined values), smaller values are preferable, so a negative correlation coefficient indicates a synergy and vice versa. Values with a box around them indicate a significant relationship at the Benjamini-Hochberg corrected level. c) Empirical point data and lines of significant relationships between pairs of ecosystem services. Green lines and boxes indicate a significant synergistic relationship. Purple lines and boxes indicate a significant trade-off relationship. Dashed lines indicate the 95% confidence interval for the predicted line. Dotted lines without a bold box indicate linear relationships that are significant at the traditional threshold of 5%, but not at the Benjamini-Hochberg corrected level.

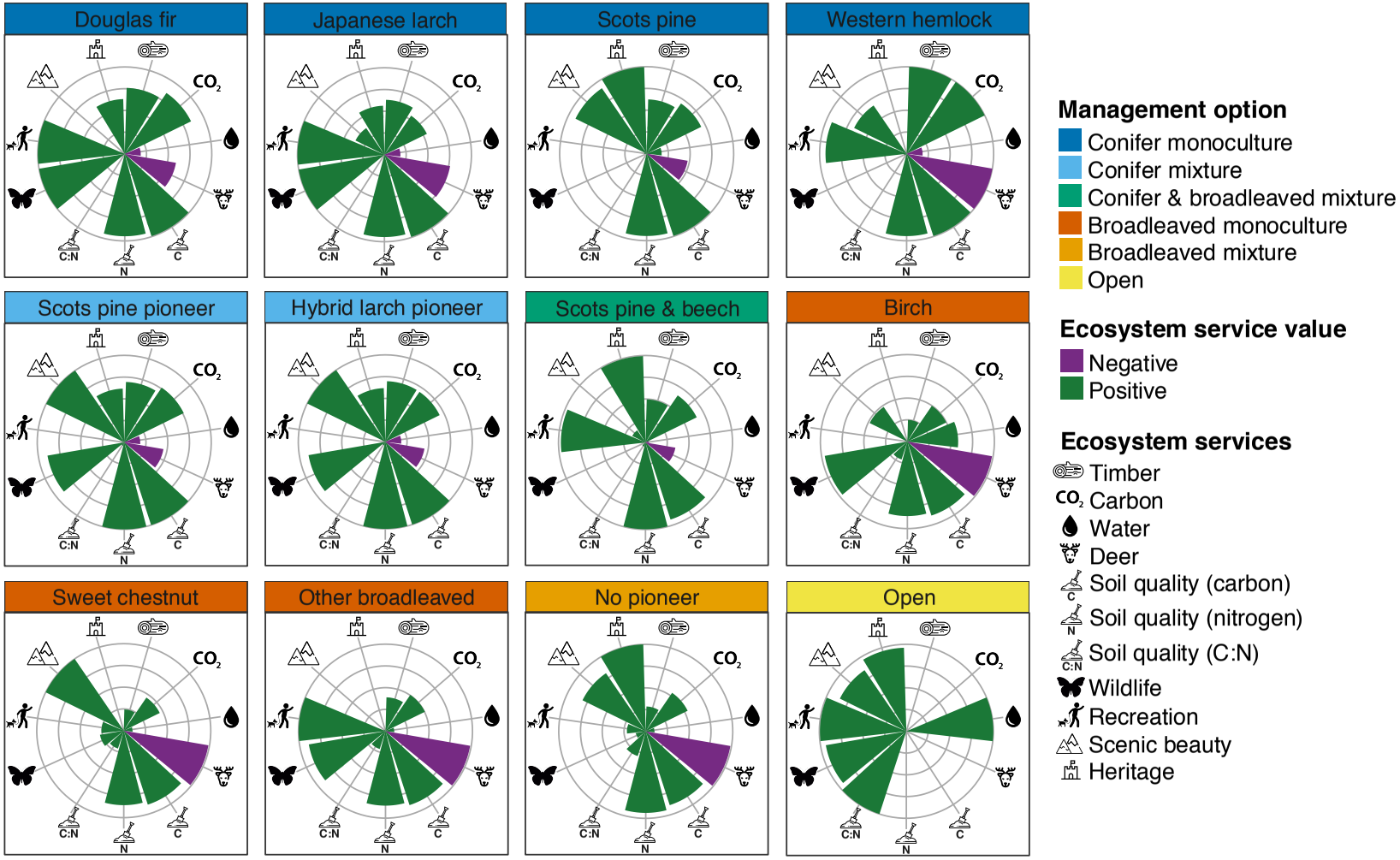

Figure 8.5: Rose plots showing the scaled ecosystem service delivery for the 12 management options with Pareto efficiency. The values are scaled between 0 (the centre of the plot) and 1 (the outer ring of the plot), with the colour of the bars indicating whether it is a positive or negative value. Each bar represents a different ecosystem service, indicated by the symbols. The background colours of the titles indicate the broad management option category (see legend).

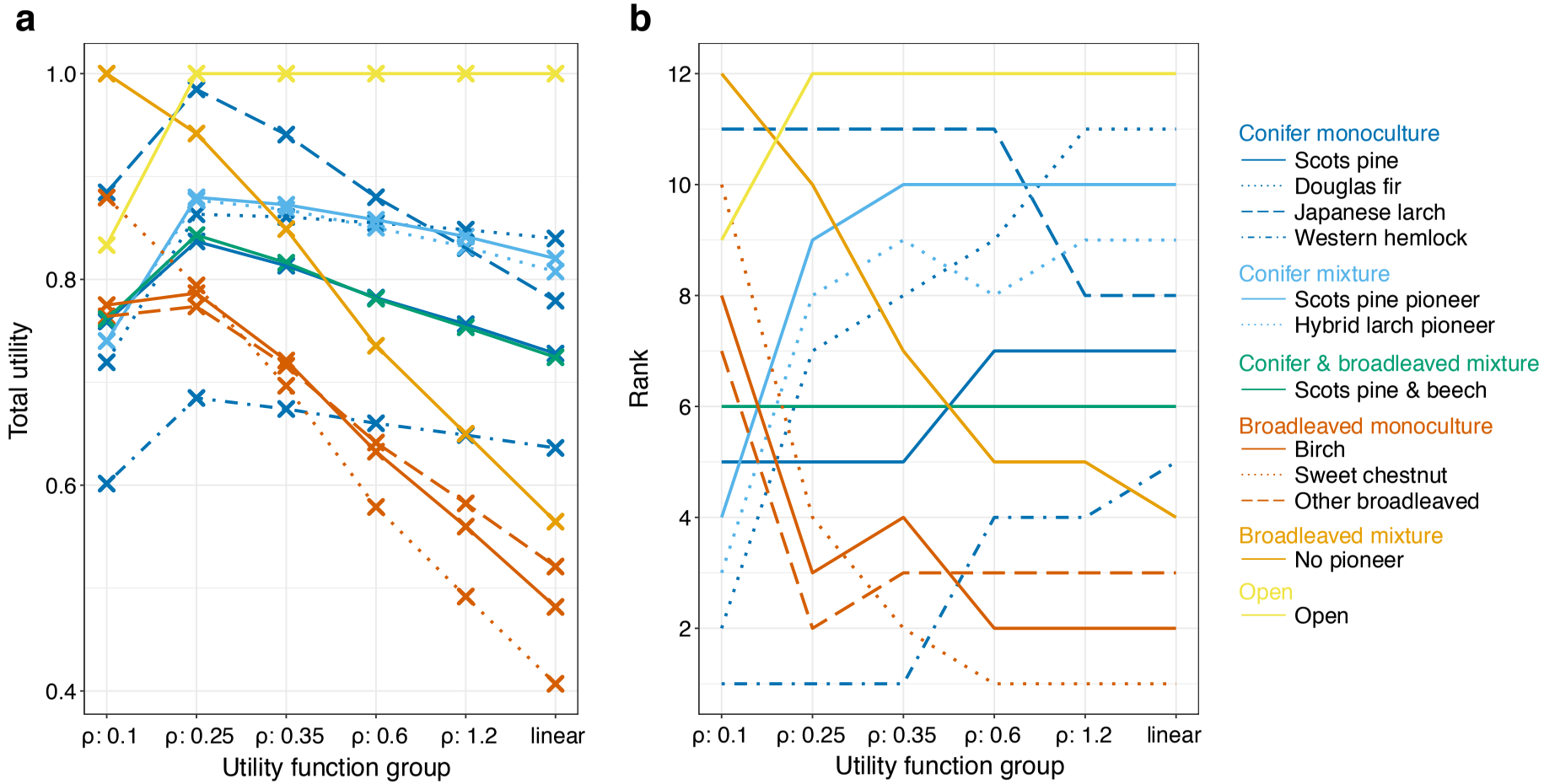

Figure 8.6: Outputs of the multi-criteria decision analysis assessing the success of different management options using different utility function curves (see Figure 8.2). a) The total utility derived from each management option for the different utility function curves. Total utility is scaled relative to the maximum utility for each utility function group. b) The relative ranks of each management option. Higher rank value indicates higher total utility value.

From the analysis of all potential landscape configurations (352,716 combinations of the 12 management options assigned in 10% blocks, see above), I identified the configuration with the highest overall utility (Figure 8.7). I found that for the linear utility function, the optimal landscape was 100% open. Open space fell to 70% of the landscape for $\rho = |1.2|$, 60% for $\rho = |0.6|$, and to 50% for all the other exponential utility functions. Conifer mixture with a Scots pine pioneer was 30% when $\rho = |0.25|$ or $|0.35|$ and 20% when $\rho = |0.1|$, $|0.6|$ or $|1.2|$. The remaining percentage was made up of conifer and broadleaved mixture when $\rho = |0.1|$ or Douglas fir monoculture for the other functions.

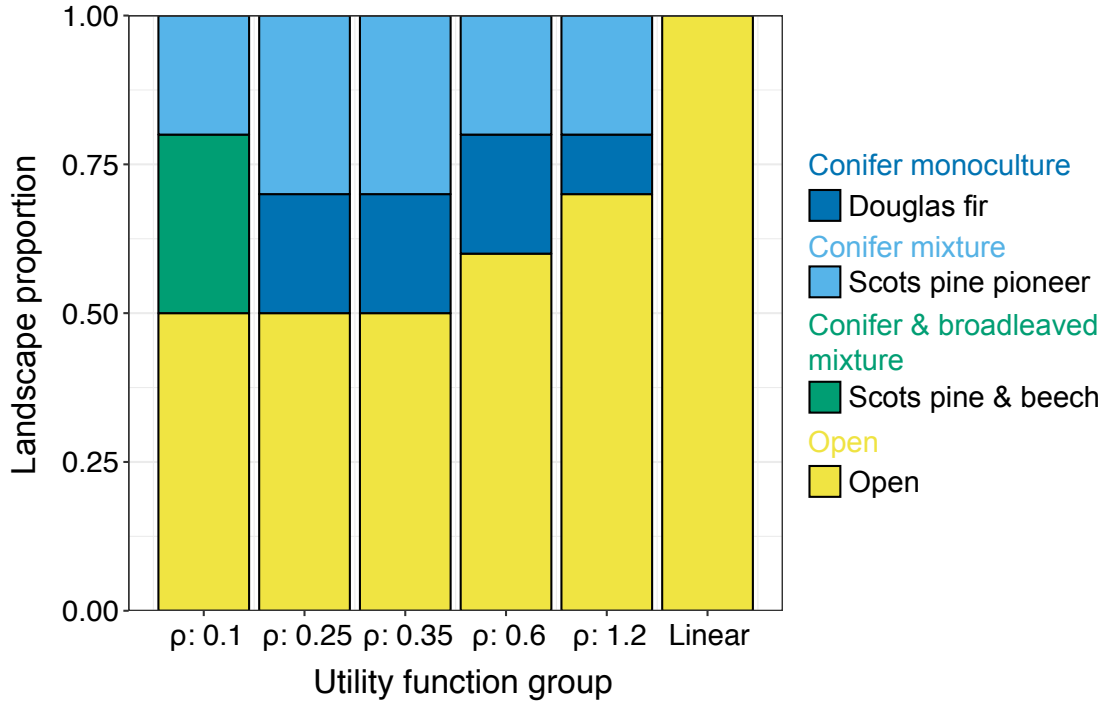

Figure 8.7: The optimal landscape configuration for each of the utility function groups.

Figure 8.8 shows the total utility values generated from all the landscape configurations tested, plotted against the landscape proportion of each management option. There were increasingly pronounced peaks in the relationship between the landscape proportion of each management option and total utility as the ρ coefficients decreased in value (i.e. was less linear). For all the conifer monoculture, conifer mixture and conifer and broadleaved mixture options, the relationship between landscape proportion and total utility became less negative as the utility functions became more linear. For all these options except western hemlock, the relationship between landscape proportion and total utility was positive for the linear utility function but overall there was a highly negative relationship for the most extreme exponential function. There was much less distinction in the overall gradient change for the broadleaved monoculture or mixture options, especially when $\rho = |0.1|$ is discounted. Open space was the only option that had clear optimal landscape proportions

with a peak in total utility, which shifted from around 0.4-0.5 for the most extreme exponential function to 1 for the linear function, mirroring the optimal landscape configurations with the maximum total utility (Figure 8.7).

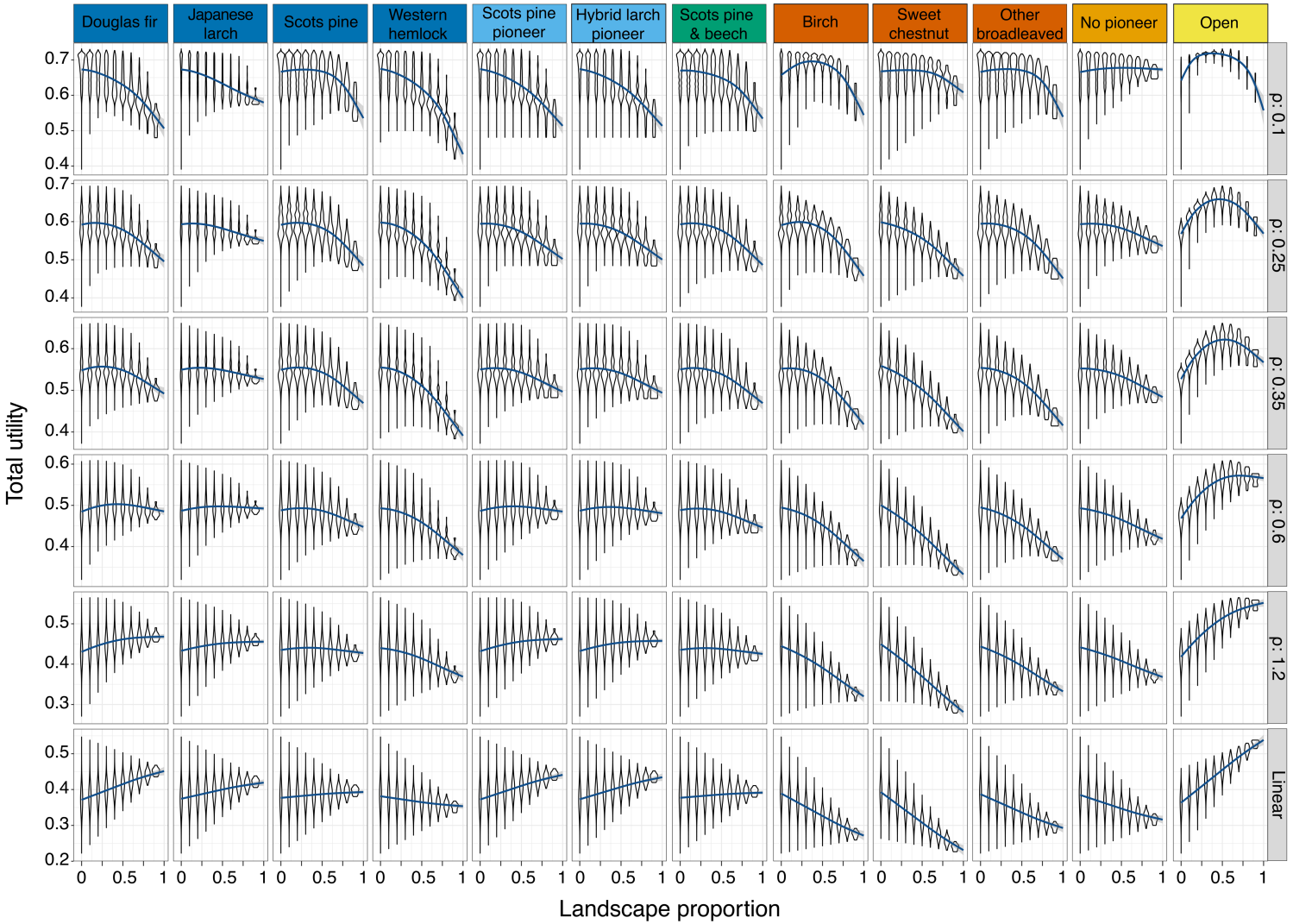

Figure 8.8: All the data from the landscape optimisations, presented by utility function and the landscape proportion of each management option. Total utility values are presented as violin plots for each 10% landscape proportion. The blue line is a smoothed line through the data points.

The weighting analysis of different ecosystem services showed some important trends. For the majority of weightings across all ecosystem services, open space was the most highly ranked management option (Figure 8.9). For open to not be the most preferred option timber and carbon had to be given at least 0.65 of the total weight, and soil quality at least 0.75 (below this open quickly dropped down the ranks to being the least preferred option). For all other ecosystem services, open was never below rank 8. Japanese larch monoculture and the conifer mixture options also tended to be highly ranked across most weightings. In particular, Japanese larch performed well as it had the best aggregated score across the ecosystem services of the four conifer monocultures (Figure 8.5). In contrast, the broadleaved monocultures were generally ranked lowly across weightings. For all ecosystem services, there was considerable reordering of ranks as weightings changed, although the manner of this differed. For some ecosystem services, such as recreation and scenic beauty, there was a relatively gradual change across weightings, whereas for other services, such as timber, carbon, water and soil quality, rankings were quite consistent until a tipping point weight (at around 0.75) when there was dramatic reordering.

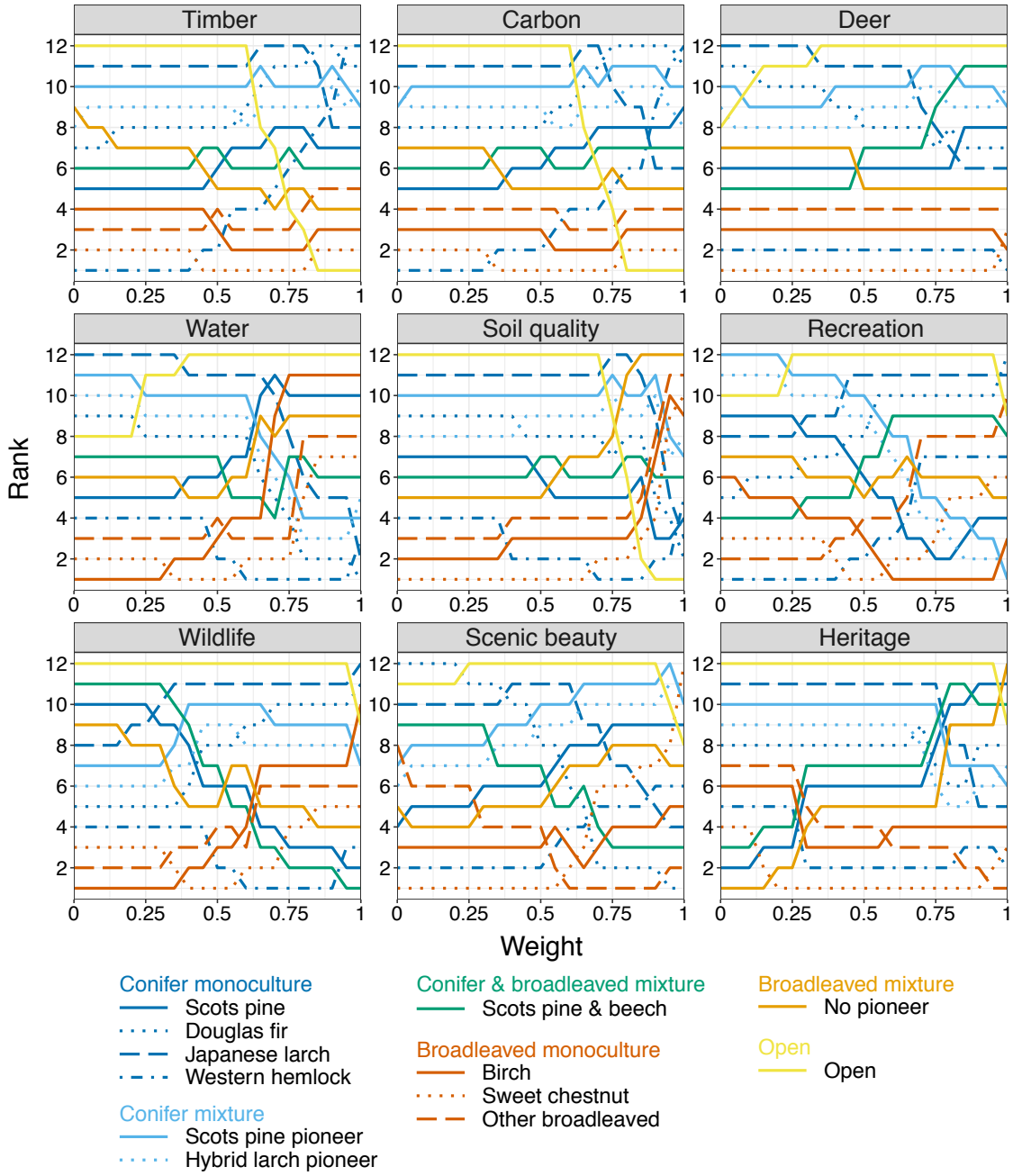

Figure 8.9: The relative ranks of the different management options according to the weight assigned to each ecosystem service. Higher rank value indicates higher total utility value. The weight refers to the ecosystem service labelled for each plot; all other ecosystem services are weighted equally. An exponential utility function of $\rho = |0.45|$ was used.

The optimal landscape configurations across different weights further emphasise the importance of open space (Figure 8.10). For the majority of weightings and ecosystem services, it constituted at least 50% of the landscape. The remainder of the landscape was generally Douglas fir monoculture or conifer mixture with a Scots pine pioneer. Interestingly, although Japanese larch ranked generally highly across weightings (Figure 8.9), it did not feature in the optimal landscape configurations (Figure 8.10). This is because open space contributed high cultural values when it occupied a high proportion of the landscape, so the difference in cultural values between conifer species became less important and instead species that were able to deliver high timber and carbon levels were selected, such as Douglas fir, western hemlock or conifer mixtures.

When different ecosystem services were assigned different utility functions according to the scale at which their benefits are felt, open space occupied the majority of the optimal landscape configuration for all groups except for when exponential functions were assigned $\rho = |0.1|$ (Figure 8.11). For this most extreme scenario (where some services were given a linear function and the remainder an extreme exponential function), the optimal landscape configuration was a mixture of Douglas fir and western hemlock monoculture with a small proportion of open space. This was because high utility values were achieved at relatively low levels for ecosystem services such as cultural services or soil quality, whereas high levels of ecosystem service delivery were required for timber, carbon and water to achieve an equivalent utility. This therefore favoured high-performing timber and carbon options (outweighing the effects of water).

When the landscape proportions of all management options were averaged for the top 5% or 10% of total utility values, the results were remarkably consistent across different utility functions (Figure 8.12 and Figure 8.13). When the same type of function was applied across all ecosystem services, open space occupied around 25-35% of the total landscape. Conifer monocultures also occupied around 25-35% and conifer mixtures a further 10-20% (with a higher proportion as the utility functions were increasingly linear). Broadleaves constituted around 10% of the total landscape for most utility functions, although higher for the most exponential functions, particularly when including the top 10% of landscape configurations. Finally, conifer and broadleaved mixtures consistently occupied approximately 6-7%.

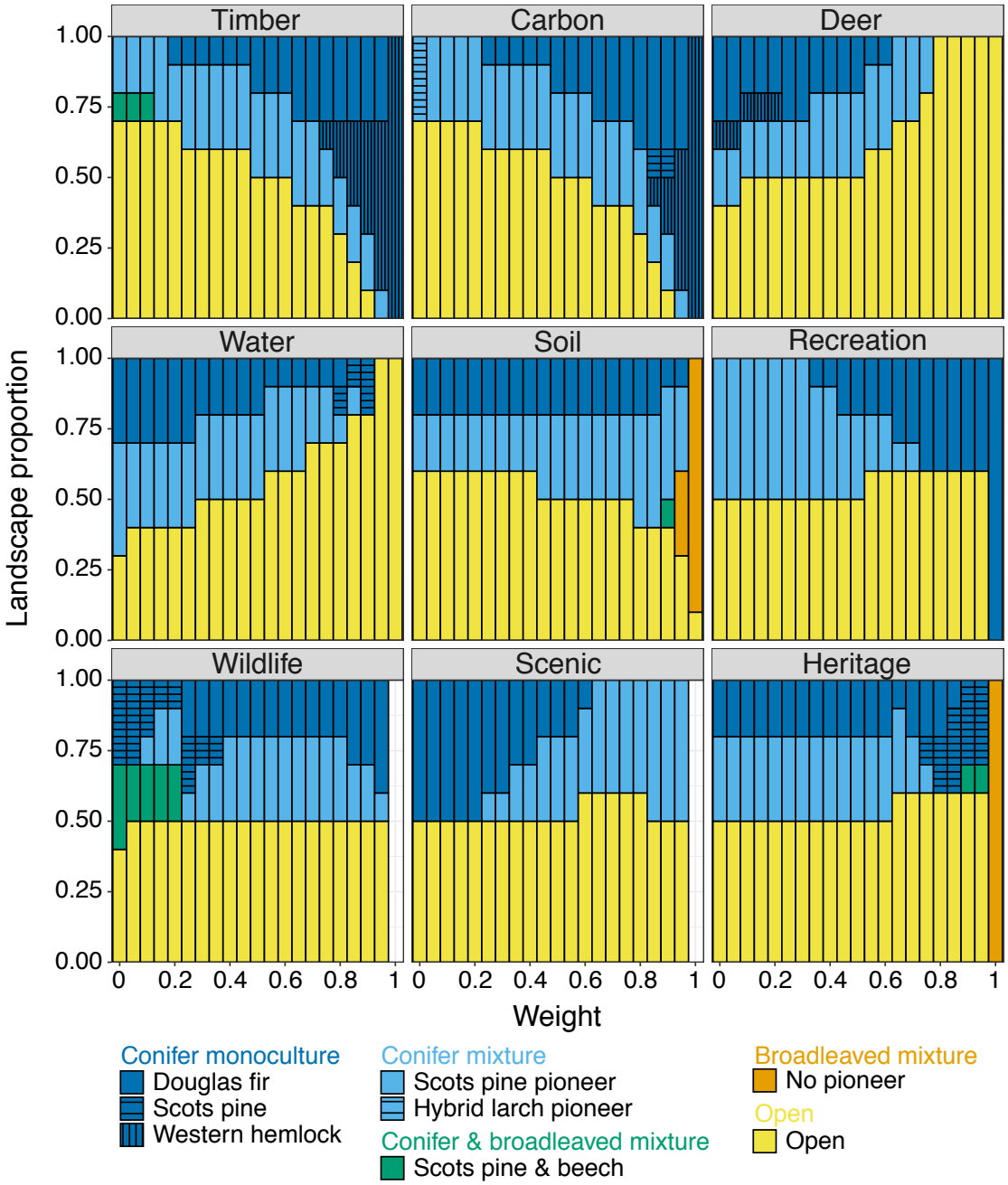

Figure 8.10: The optimal landscape configuration for different weightings assigned to each ecosystem service. The weight refers to the ecosystem service labelled for each plot; all other ecosystem services are weighted equally. An exponential utility function of $\rho = |0.45|$ was used.

When different functions were applied according to the scale of the ecosystem service benefit, there were greater differences between the utility function groups (Figure 8.12 and Figure 8.13). When ρ = |0.25|, |0.35|, |0.6| or |1.2|, the overall average landscape compositions were similar to those when a universal function was applied, although conifers had a slightly higher and open a slightly lower landscape proportion. However, at the more extreme exponential functions, conifers were increasingly favoured. When ρ = |0.1|, open space constituted less than 15% of the landscape, and conifer monocultures were approximately 50%. Nevertheless, the similarities in landscape composition, across the different utility function groups and when functions were applied universally or differently between ecosystem services, are striking, with a clear overall pattern. This is particularly so for those groups that are more realistic (i.e. those not at the extreme exponential or linear ends).

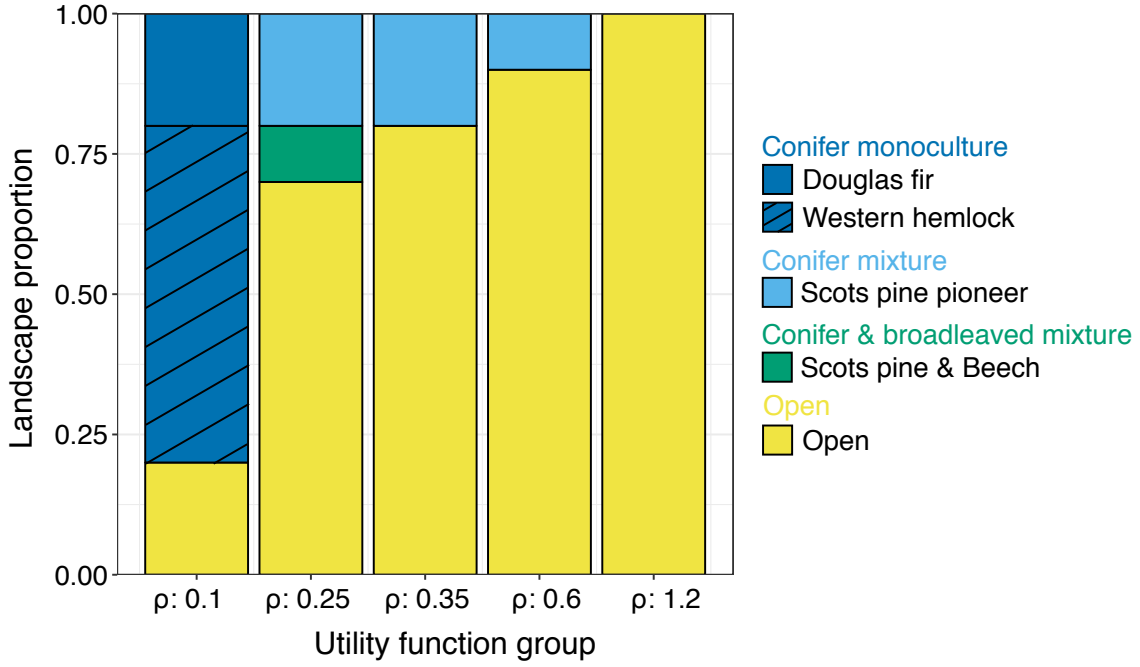

Figure 8.11: The optimal landscape configuration when ecosystem services are assigned different utility functions according to the scale of their benefits. The utility function group corresponds to the ecosystem services that are assigned an exponential curve.

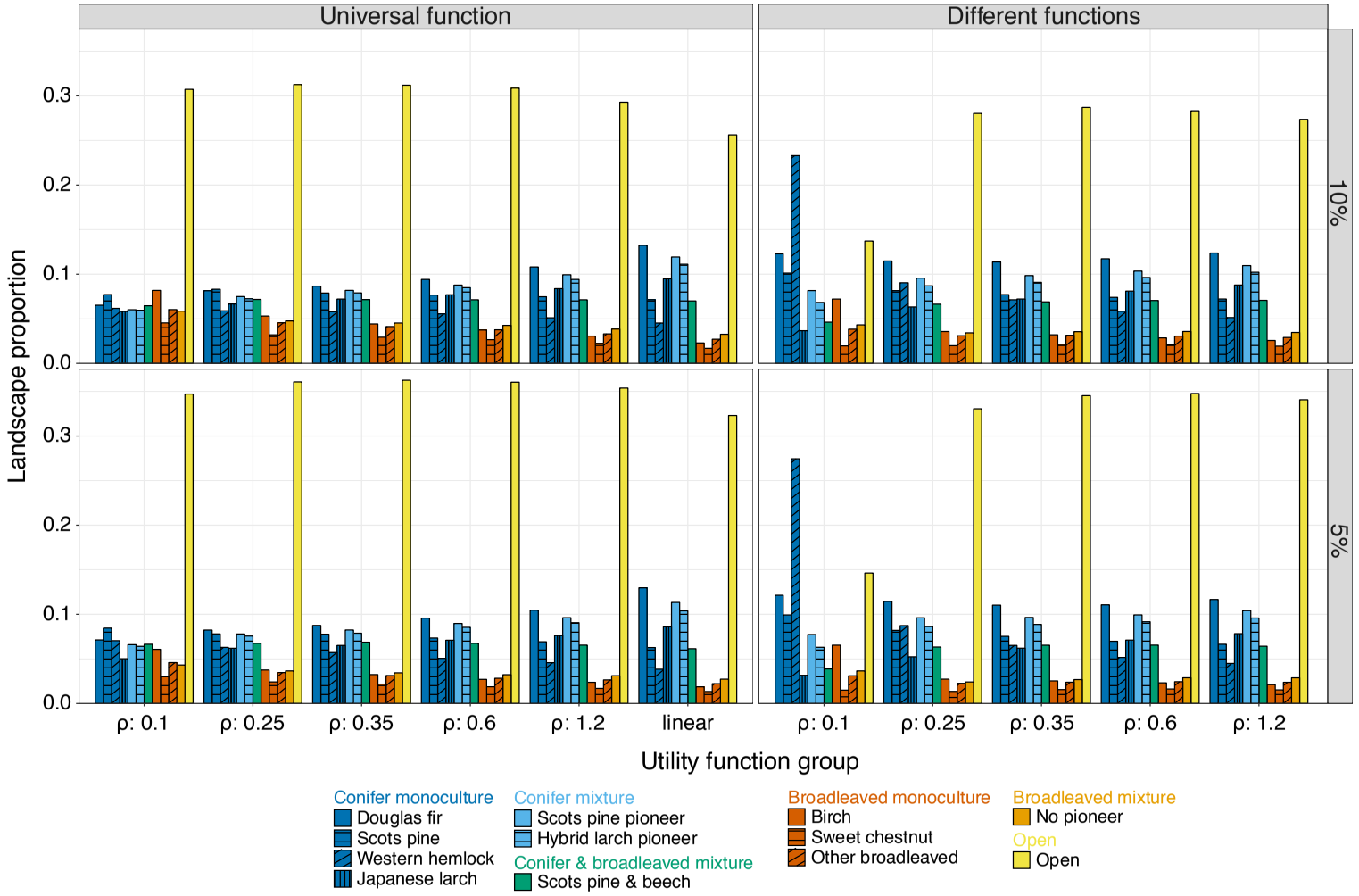

Figure 8.12: The mean landscape proportions for each management option for the top 10% (top panels) or 5% (bottom panels) of total utility values across all landscape configurations. The left panels correspond to solutions when all ecosystem services are assigned the same utility function; the right panels correspond to solutions when ecosystem services are assigned different utility functions according to the scale of their benefits.

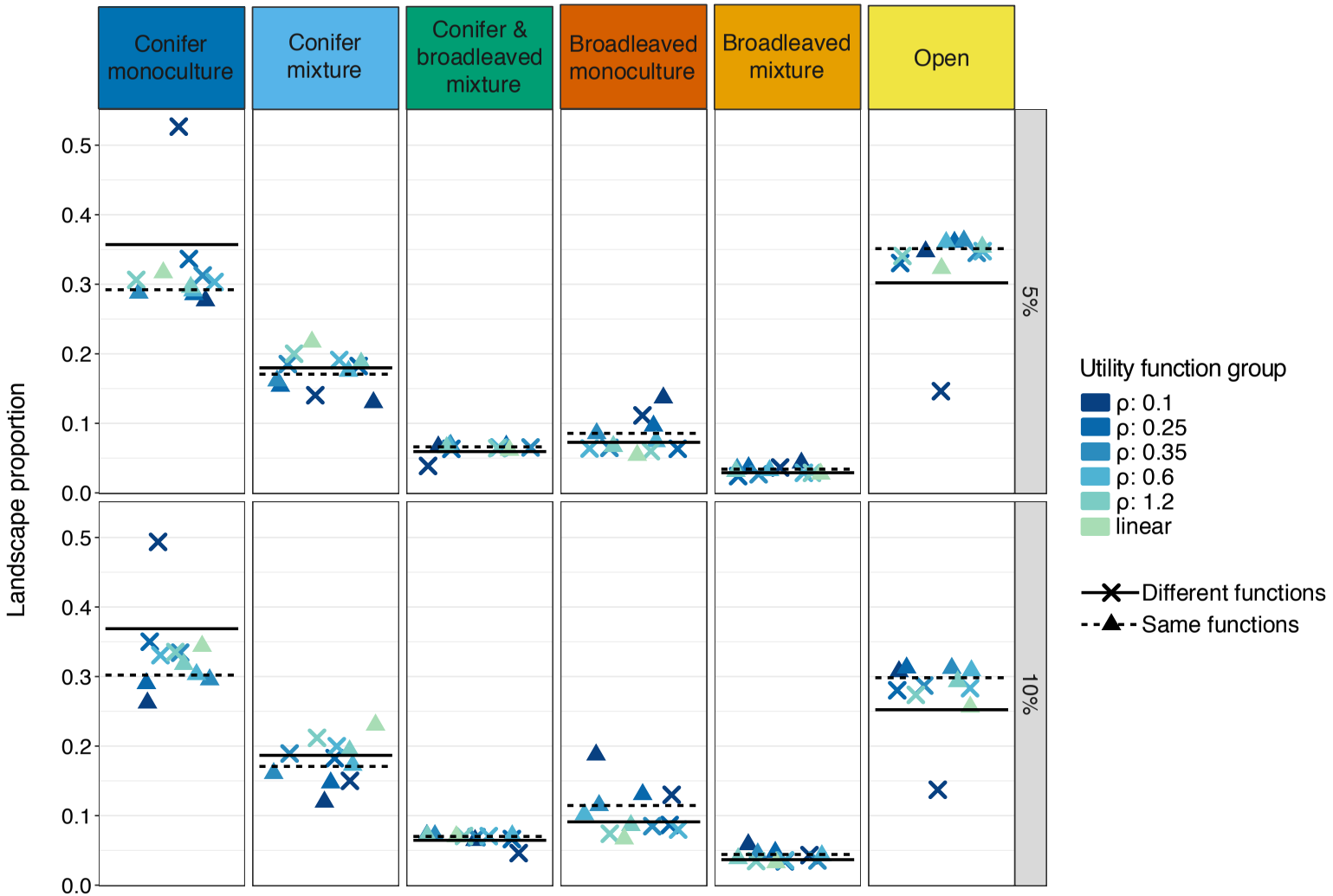

Figure 8.13: The mean landscape proportions of broad management options. Line type and point symbol indicate whether all ecosystem services are assigned the same or different utility functions. Colours of points indicate the utility function group (when ecosystem services are assigned different utility functions, this corresponds to the utility function of those ecosystem services that have exponential curves). The horizontal lines indicate the means of the proportions.

DISCUSSION

Incorporating analysis of ecosystem service delivery into decision-making is essential for achieving a sustainable future and can greatly increase societal benefits from natural resource use [21,250,428,450]. Different habitats deliver different combinations and amounts of ecosystem services, so coordinated landscape strategies are required [451]. However, guidance and recommendations for how this can be achieved is lacking, and there is limited integration of the ecosystem services framework into practical management and planning decisions [26,34,324].

A useful first step is to analyse the trade-offs and synergies between ecosystem services, which is quantified in surprisingly few studies [34,42,274]. Furthermore, it is essential to consider a representative range of ecosystem services; cultural services in particular are often missing [35,42,257]. Forests can deliver a wide range of ecosystem services, particularly in a landscape matrix that also includes areas of open habitat [452]. However, no single type of forest management can simultaneously maximise all ecosystem services and varied relationships between ecosystem services are expected [46,282,430]. Across a comprehensive suite of 11 ecosystem services, I found a total of 18 significant relationships, of which 9 were trade-offs and 9 were synergies. This is an important finding, as generally trade-offs receive more attention in the literature [42,323]; in this study the two types of relationship are actually equally prevalent. Furthermore, there was no obvious distinction in whether relationships were trade-offs or synergies between the different types of ecosystem service (provisioning – timber, deer, water; regulating – carbon, soil quality; cultural – wildlife, recreation, scenic beauty, heritage). This is in contrast to the findings from a recent review that synergies were more common within regulating and cultural services while trade-offs were more common between regulating and provisioning services [435].

The nature and extent of these relationships was illustrated when the management options were reduced to just those with Pareto efficiency. As would be expected, the greatest difference was between the open space option and all other forestry options. Open space was the best option for water supply for human use, which was greatly reduced or negative for all the other options, and it did not deliver any negative deer value. However, open space did not deliver any timber or carbon value, which was generally greatest in the conifer options. Differences between cultural ecosystem services were more variable. These generalisations are familiar and well-understood by forest managers, but this analysis is helpful in formalising the extent of differences and similarities between different management options. Furthermore, by identifying and discarding potential options that do not have Pareto efficiency, the decision process can be greatly streamlined. However, the situation is still complex, and clearly a combination of open space and forestry is necessary to maximise overall benefits. To generate meaningful recommendations, the multi-criteria decision analysis is essential.

Most studies considering the effects of land use on ecosystem services focus on a set of particular landscape scenarios, and evaluate differences between these alternatives [42]. While this has considerable use when only certain scenarios are possible, this is otherwise limiting, and often represents just a subset of realistic possibilities. It can be informative to understand how a landscape might be designed if maximising ecosystem services delivery is the only objective or consideration. This can highlight the extent of the differences between more optimal landscape scenarios and those which are currently under consideration, potentially prompting more imaginative landscape design or longer-term strategic objectives. However, to be truly useful for decision-makers, such analysis must be grounded in realism and should consider management options that are both possible and probable, rather than those which may be excellent for ecosystem service delivery but unachievable for other reasons. Hence, the importance of engaging stakeholders in the initial design phase. Multi-criteria decision analysis can then incorporate other considerations and constraints, such as the need to prioritise a certain ecosystem service for economic reasons, through altering the weights and utility functions [443–445].

As found in other studies, both the weights and the utility functions changed the results of the multi-criteria decision analysis [436,447]. Open space and conifer options were favoured by all utility functions except the most extreme exponential functions, when broadleaves performed better (Figure 8.6). This was because broadleaved options tended to deliver more ecosystem services at lower levels (so were favoured when low values generate high utility), whereas conifer options delivered higher levels of generally fewer ecosystem services. The most striking finding from the analyses of weights and utility functions was the universal importance of open space – ecosystem services that are favoured by forested options (such as timber, carbon and soil quality) had to be weighted very highly, or the most extreme exponential function used, to displace open space from the top-ranking position (Figure 8.6 and Figure 8.10). In a normal sensitivity analysis of multi-criteria decision analysis, this would be a successful result, indicating that the overall 'best' management option is robust to changes in perspectives and values, which are inevitable in long-term land management planning [34,433,448]. These results indicate that if one land parcel was to be converted, open space would be the best option to choose. However, this outcome is not so useful for practical decision-making purposes where the objective is to determine an ideal landscape composition rather than a single preferred option. Clearly, converting the entire landscape to open space would be detrimental to ecosystem services such as timber and carbon sequestration. Therefore, if multiple land parcels were to be converted, we would expect there to be a point when it would be more beneficial to choose an alternative option to open space that could deliver other ecosystem services.

Many multi-criteria decision analysis studies assume a simple linear relationship between the attribute being measured and the value that it generates [446]. In this situation, the option that is most

highly ranked in the assessment will always be favoured regardless of how much of the landscape is already attributed to that option (as demonstrated in Figure 8.7 where the optimal landscape configuration is 100% open space for the linear utility function group). Curved utility functions, which are more realistic representations of value and have decreasing marginal values as ecosystem service delivery increases, are necessary to explore how landscape compositions may include multiple management options. I found that open space remained the most important landscape component for optimal scenarios regardless of the utility function used (at least 50% of the landscape; Figure 8.7). As for the analysis of the best management option, this result was robust to differences when weightings were changed for each ecosystem service, with open space accounting for at least 50% of the landscape for most weighting options (Figure 8.10).

The relative importance of open space was even more dramatic when different utility functions were assigned to different ecosystem services based on the scale at which their benefits are felt, with at least 70% open space being in the optimal landscape composition for all utility function groups except the most extreme exponential (Figure 8.11). As timber, carbon and water were assigned a linear utility function, this decreased their utility relative to other ecosystem services, thus increasing the overall value of open space relative to forestry options. Interestingly though, when the most extreme exponential utility function was applied to the local-scale ecosystem services, high utility values could be achieved at such low levels of local-scale ecosystem services that instead timber, carbon and water became more important discriminants between management options. This resulted in a landscape dominated by conifer monoculture options. This method of assigning different value functions to ecosystem services serves to distinguish between those services that can only be produced locally and those that can be produced elsewhere, which is an important and useful distinction. However, this type of prioritisation may lead to the generation of off-site effects, whereby local benefits are maximised by displacing certain land management types to other areas [34,453]. For example, increasing open space for local benefits but assuming that more forested areas (which can deliver timber and carbon benefits) can be put elsewhere, even though this may cause a reduction in localised benefits at another site. This is a complex issue, but it is important to bear in mind when assessing landscape composition alternatives.

These analyses find the single optimal landscape composition that delivers the greatest overall utility. However, there are alternatives that still deliver very high utility, which are important to explore, as not all stakeholders are likely to benefit equally from one solution and because the true optima may not be feasible or appealing to the land manager. In this case study, converting a forested landscape to be mostly or entirely open space is clearly unlikely to be an amenable suggestion, even if an open space component is recognised to be an important part of the landscape. When the mean percentage composition of management options across the landscape was calculated for the top 5% or 10% of utility values, the results were remarkably consistent across

different utility function groups (Figure 8.12 and Figure 8.13). The overall mean percentage composition of each management option was also fairly consistent when either the same or different utility functions were applied to ecosystem services depending on the scale of their benefits, except for the most extreme of the different utility functions. This resulted in a decrease in open space and an increase in conifer monoculture mean percentage composition, although the other management options were much more similar (Figure 8.13). In general, open space was still the highest individual management option, although around 65-75% of the landscape remained forested. Conifer monocultures dominated the forestry component, followed by mixtures and a smaller component of broadleaves. In summary, the ideal landscape would comprise around 35% open space, 30% conifer monoculture, 18% conifer mixture, 7% conifer and broadleaved mixture, 7% broadleaved monoculture, and 3% broadleaved mixture. Alternatively, the open space component could be reduced by around 5% in favour of increasing conifer monocultures or broadleaves if the top 10% rather than 5% of utility values was acceptable as a guideline. While still highlighting the importance of open space for ecosystem services in this particular landscape, this result aligns much better with expectations for a multi-purpose, managed forest landscape. Furthermore, the consistency in this landscape composition across the utility functions, particularly for the intermediate functions that are more realistic, in combination with the lack of effect of the weightings, gives great confidence in this result at a realistic management recommendation to maximise ecosystem service delivery.

In chapter 7, I evaluated the effects of management options on biodiversity. The relationship between biodiversity and ecosystem services is complex; biodiversity can regulate the ecological processes that give rise to ecosystem services, as well as be a final ecosystem service or a good [13]. In the multi-criteria decision analysis, I included the cultural value of wildlife as an ecosystem service. However, the biodiversity that people value and that generates cultural ecosystem services is often biased to a subset of species [14]. It is therefore useful to also include a more traditional assessment of biodiversity, to determine how and whether land management planning for ecosystem services and biodiversity conservation align. I concluded from my biodiversity analysis that bird diversity is likely to be favoured by between-stand diversity, rather than within-stand structural heterogeneity. In particular, a variety of stand ages, including areas of open space, was found to be important. This complements findings from this multi-criteria decision analysis, which recommends a high proportion of open space and conifer monocultures, in addition to a smaller proportion of other habitats such as mixtures and broadleaves. In identifying the management options with Pareto efficiency for ecosystem services, conifers managed through rotational clearfell were discarded in favour of continuous-cover forestry that had higher carbon values. However, the differences between rotational clearfell and continuous-cover were not evaluated for other ecosystem services. In light of this, and considering the results from the biodiversity analysis, I

would recommend that the conifer monoculture components of the overall landscape are managed through a mixture of both management strategies. This would create a diversity of single-aged stands of varying age classes in addition to more complex stand structures. The overall landscape recommended for maximising ecosystem services would then have high between-stand diversity, benefiting bird diversity, and suggesting that both ecosystem service and biodiversity conservation objectives are compatible. Based on this study, the overall recommendation for future management of Thetford Forest to maximise ecosystem services and biodiversity would be for around a third to be open space, half to be conifers (with a ratio of mixtures to monocultures of around 1:2) managed through a combination of both rotational clearfell and continuous-cover, and the remainder as conifer and broadleaved mixtures, broadleaved monocultures and a small broadleaved mixture component.

Of course, a key caveat to this conclusion is that the biodiversity analysis included only birds; other taxonomic groups may require different types of habitat management. For example, the open habitat network within Thetford Forest is known to be particularly important for a rare assemblage of plants and invertebrates [61,62]. However, a recommendation for a third of the landscape to be open space exceeds current conservation targets for these groups. Given that the overall landscape composition recommended for ecosystem service delivery is fairly diverse, there is significant potential to refine the exact strategy to incorporate other biodiversity management considerations.

Further improvement to the multi-criteria decision analysis could be the consideration of the effect of spatial variation across the landscape [42]. The Thetford Forest landscape is a largely continuous block, and the effects of management will be equivalent for many ecosystem services across the area. However, some external factors will have a spatial influence on ecosystem service delivery, such as the effect of soil type on tree growth and timber yield, which would be beneficial to include in the analysis as a next step. The utility functions that I used represented a range of hypothetical values and perspectives. The engagement of stakeholders to elucidate the true functions would clearly be a useful future avenue of research. For example, in reality there is likely to be a minimum threshold of service delivery before any utility is reached, such as the lowest economically viable level of timber production [444,446]. The analysis for each ecosystem service was detailed and specific to the landscape, but of course all analysis has a certain level of uncertainty associated with it. Incorporating the level of uncertainty associated with each ecosystem service could improve the overall ecosystem service evaluation [34]. Although the best efforts were made to ensure that ecosystem service quantifications were as accurate as possible, the final results are only as good as the data input and so need to be interpreted with their associated caveats in mind (which are discussed in the relevant chapters).

To incorporate the ecosystem services framework into practical decision making, research needs to be grounded in realistic scenarios, consider a comprehensive range of ecosystem services and their

relationships, and ideally provide specific recommendations for land managers and decision-makers [34,36,39]. In this study, I have incorporated all these considerations and demonstrated that it is possible to generate a sensible management recommendation to improve ecosystem service delivery in the landscape by focusing on a subset of the best performing potential landscape configurations. By explicitly exploring a range of utility functions and weightings, which cover the most extreme and more realistic possibilities, I have been able to uncover in detail how values and perspectives alter conclusions. Importantly, the overall results are robust to these factors and gives confidence to the recommendations, which is especially significant given that the potential supply and demand for different ecosystem services will inevitably change in future. The next step for this analysis would be to more formally include constraints in the analysis, such as by determining which parts of the landscape can be realistically changed in the short-term to achieve higher ecosystem service delivery, and to incorporate spatial variation across the landscape. In the meantime, this analysis represents an important step forward in the practical application of ecosystem services, serving as a case study for a promising avenue to incorporate ecosystem services into land management and planning.

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Appendix A: Chapter 2

Appendix table A.1: Species, yield classes and spacings with existing timber yield models.

Type of species	Species	Yield class		Spacing (m)	
		Minimum	Maximum	Available for all yield classes	Available for subset of yield classes
Broadleaved	Beech	4	10	1.2	
Broadleaved	Oak	4	8	1.2	
Broadleaved	Poplar	4	14	2.7, 4.6, 7.3	
Broadleaved	Roble	10	18	1.7	
Broadleaved	Sycamore	4	12	1.5	
Conifer	Corsican pine	6	20	1.4, 2, 2.5, 3	4.5
Conifer	Douglas fir	8	24	1.7	
Conifer	European larch	4	12	1.7	
Conifer	Grand fir	12	30	1.8	
Conifer	Japanese larch	4	14	1.7, 2.4	1.2, 1.8
Conifer	Lodgepole pine	4	14	1.5, 2, 2.4, 3	1.8, 2.2, 2.6
Conifer	Noble fir	10	22	1.5	
Conifer	Norway spruce	6	22	1.5, 2, 2.4, 3	0.9, 1.4, 1.8
Conifer	Scots pine	4	14	1.4, 2, 2.4, 3	0.9, 1.8, 2.5, 4.5
Conifer	Sitka spruce	6	24	1.7, 2, 2.4, 3	0.9, 1.4, 1.8, 2.1, 2.2, 2.6
Conifer	Western hemlock	12	24	1.5	
Conifer	Western red cedar	12	24	1.5	

ASSESSMENT OF THE TIMBER INTERPOLATION METHOD ACCURACY

To calculate the timber production potential of different species and yield class combinations at a universal spacing, I interpolated between existing yield curves. To formally test the accuracy of these techniques, I removed certain planting spacings from the dataset and predicted their timber production potential using these methods. I then calculated the percentage difference between the actual and predicted timber production potential values.

To assess interpolation method 1 (see Methods section of chapter 2), I removed the data for the 2 m planting spacing for Corsican pine, lodgepole pine *Pinus contorta*, Norway spruce, Scots pine and Sitka spruce *Picea sitchensis*, and predicted the timber production potential at 2 m using the remaining three planting spacings for each species. To assess interpolation method 2 (see Methods section of chapter 2), I removed the intercept data from one species and recalculated the family of cubic linear functions for the remaining species' intercept data (as in Figure 2.2d). For the removed species, I used the intercept value of each planting spacing (except 2 m) in turn to predict the intercept value for a spacing of 2 m (as in Figure 2.2g) and the subsequent timber production potential value. I repeated this analysis for each of the same five species listed above to assess interpolation method 1.

For interpolation method 1, the mean percentage difference between the actual and predicted timber production values was 0.58% (standard deviation: 0.39%), with a maximum percentage difference of 1.8%. For interpolation method 2, the mean percentage difference was 1.02% (standard deviation: 1.12%), with a maximum percentage difference of 5.98%.

Appendix table A.2: Management options used in carbon modelling (highlighted cells). CCF corresponds to continuous-cover forestry.

Description	Species		Clearfell	CCF	Underplanting	
					Clearfell	CCF
Conifer monoculture	Corsican pine					
	Douglas fir					
	Hybrid larch					
	Japanese larch					
	Scots pine					
	Serbian spruce					
	Western hemlock					
	Western red cedar					
	Other conifer					
Conifer mixture	Scots pine pioneer	Douglas fir				
		Western hemlock				
		Western red cedar				
		Japanese cedar				
		Serbian spruce				
	Hybrid larch pioneer	Douglas fir				
		Western hemlock				
		Western red cedar				
		Japanese cedar				
		Serbian spruce				
	Scots pine pioneer	Douglas fir, western hemlock				
		Douglas fir, western red cedar				
		Douglas fir, Japanese cedar				
		Western hemlock, western red cedar				
		Western hemlock, Japanese cedar				
		Western red cedar, Japanese cedar				
		Douglas fir, western hemlock, western red cedar				
		Douglas fir, western hemlock, Japanese cedar				
		Douglas fir, western red cedar, Japanese cedar				
		Western hemlock, western red cedar, Japanese cedar				
		Douglas fir, western hemlock, western red cedar, Japanese cedar				
	Hybrid larch pioneer	Douglas fir, western hemlock				
		Douglas fir, western red cedar				
		Douglas fir, Japanese cedar				
		Western hemlock, western red cedar				
		Western hemlock, Japanese cedar				
		Western red cedar, Japanese cedar				

		Douglas fir, western hemlock, western red cedar				
		Douglas fir, western hemlock, Japanese cedar				
		Douglas fir, western red cedar, Japanese cedar				
		Western hemlock, western red cedar, Japanese cedar				
		Douglas fir, western hemlock, western red cedar, Japanese cedar				
Broadleaved monoculture	Birch					
	Eucalyptus					
	Sweet chestnut					
	Other broadleaved					
Broadleaved mixture	Birch pioneer	Beech, oak, Sycamore				
	Sweet chestnut pioneer	Beech, oak, Sycamore				
	No pioneer	Beech, oak, Sycamore				
	Birch & sweet chestnut pioneer	Beech, oak, Sycamore				
Conifer and broadleaved mixture	Scots pine & beech					
	Scots pine & oak					

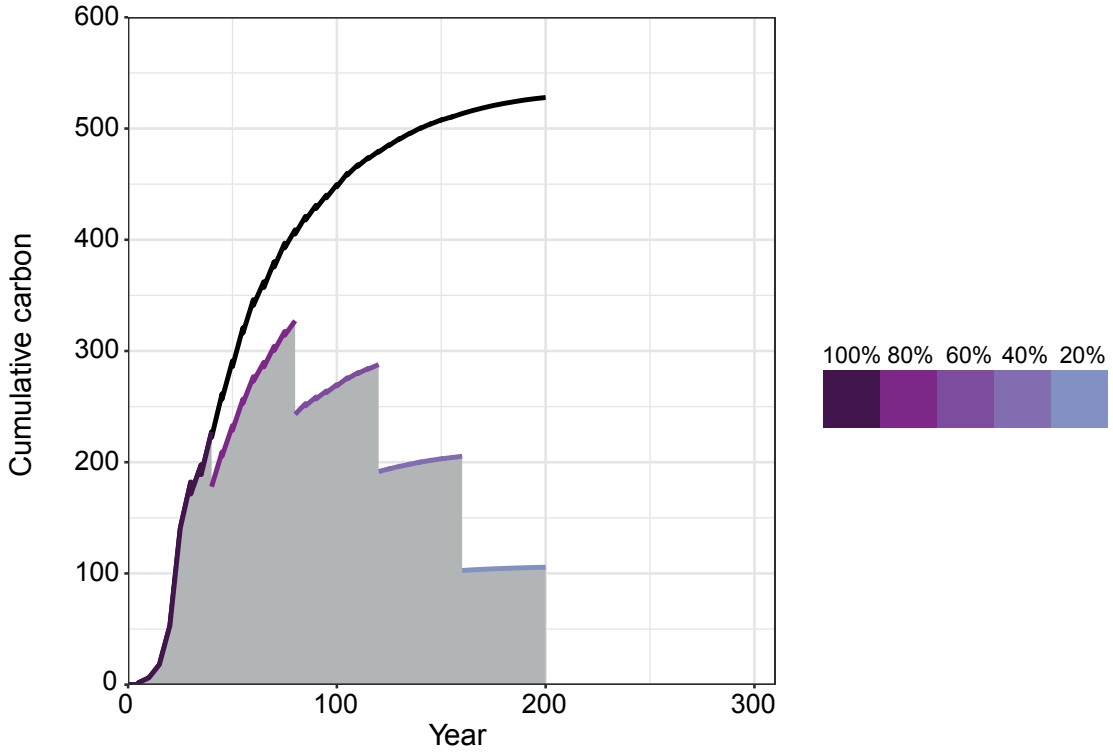
DETAILED GRAPHICAL REPRESENTATIONS OF CARBON MODELLING FOR CONTINUOUS-COVER AND CLEARFELL MANAGEMENT OPTIONS

Continuous-cover

Modelling for continuous-cover management options is separated into the first and subsequent (secondary) stands. This is because the first stand is established covering the entire area, but then decreases by 20% of the area every 40 years. All subsequent (secondary) stands occupy 20% of the total area throughout their life-cycle.

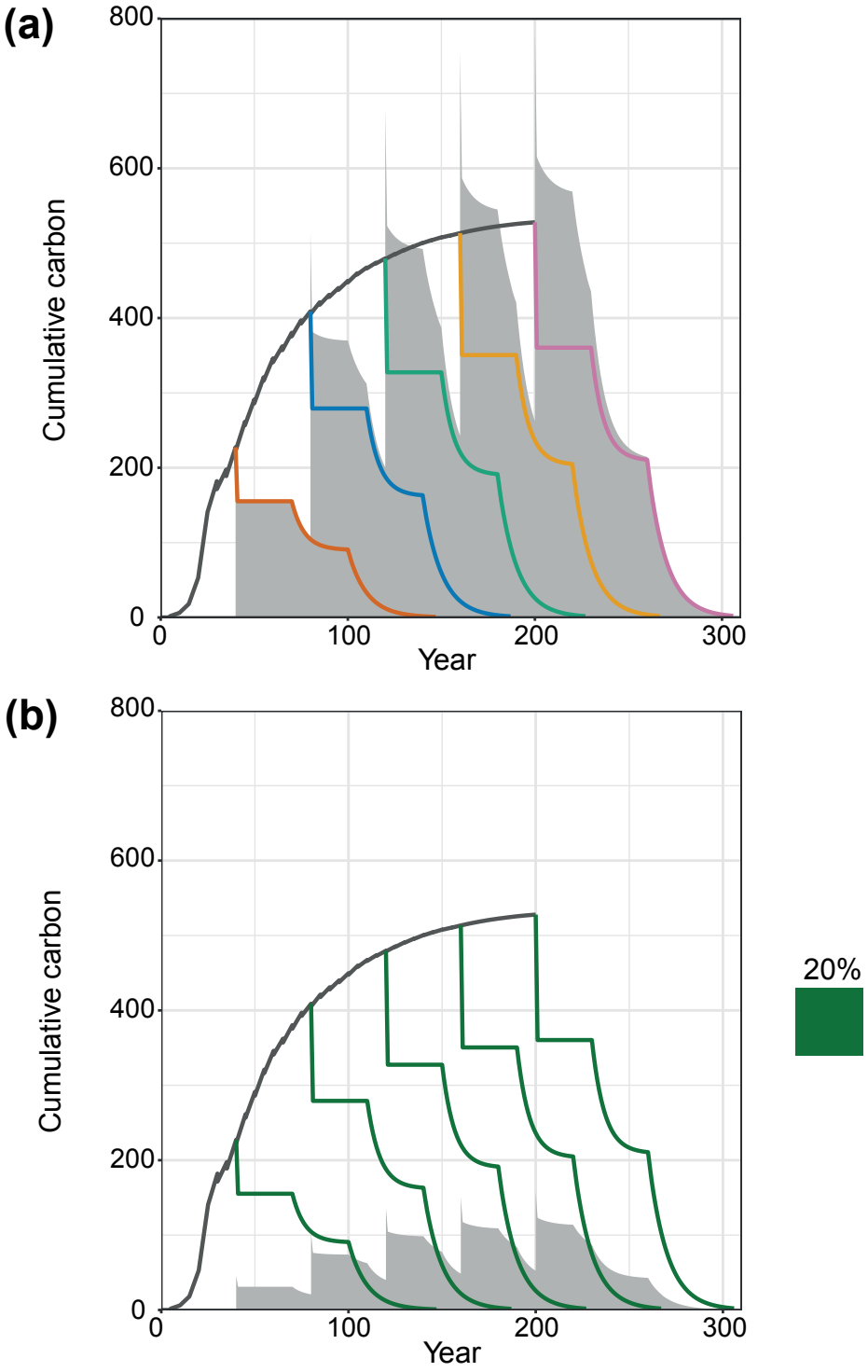
First stand

Standing biomass



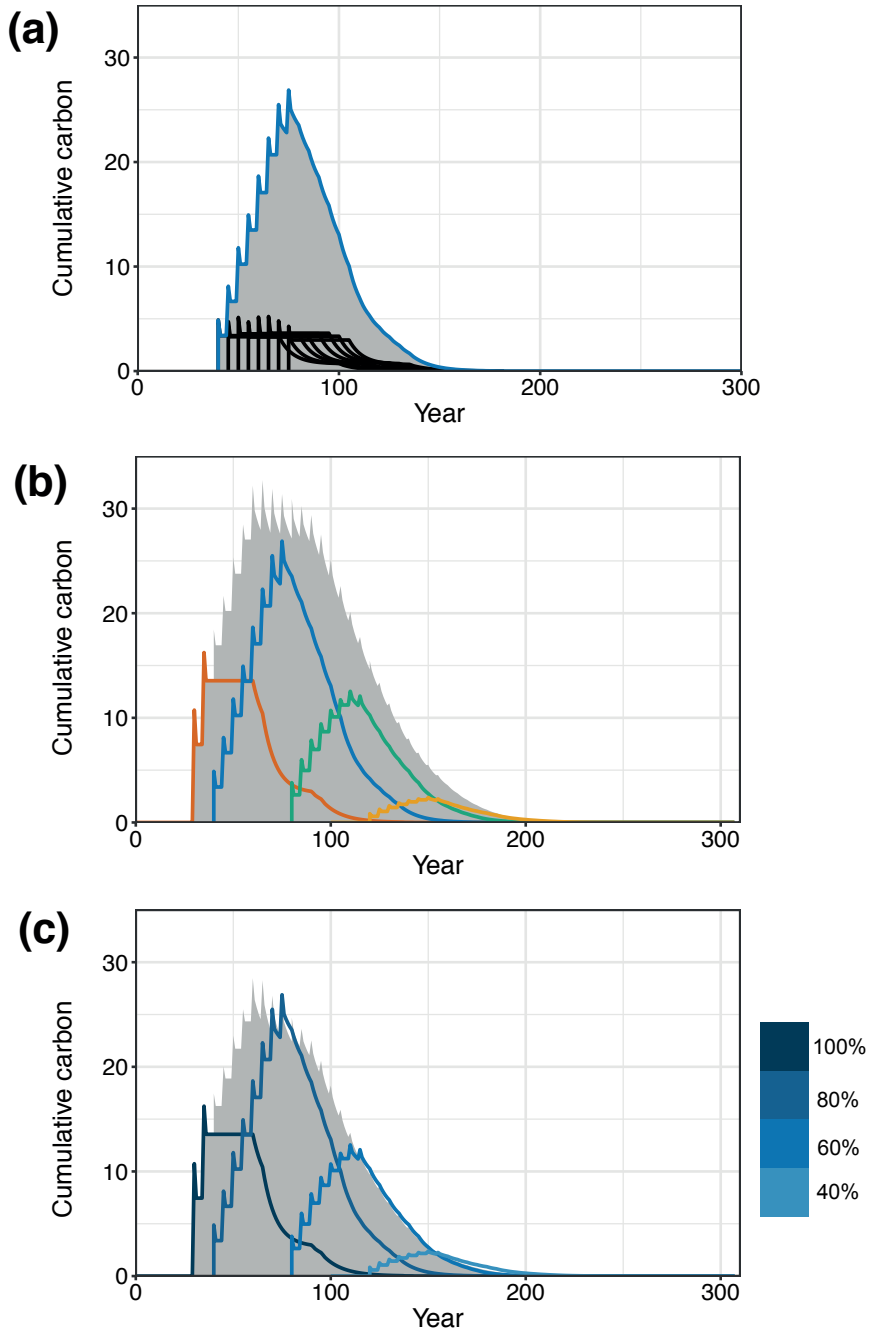
Appendix figure A.1: Carbon is accumulated in standing biomass, as indicated by the black line. 'Saw-teeth' are the result of the removal of carbon in 5-yearly thinning events. 20% of the stand is removed after every 40 years in the continuous-cover cycle. The grey shaded area shows the overall carbon sequestered in standing biomass over time, taking into account the reduction in total volume every 40 years. The shading of the purple line indicates the proportion of the original stand left.

Decay from felling



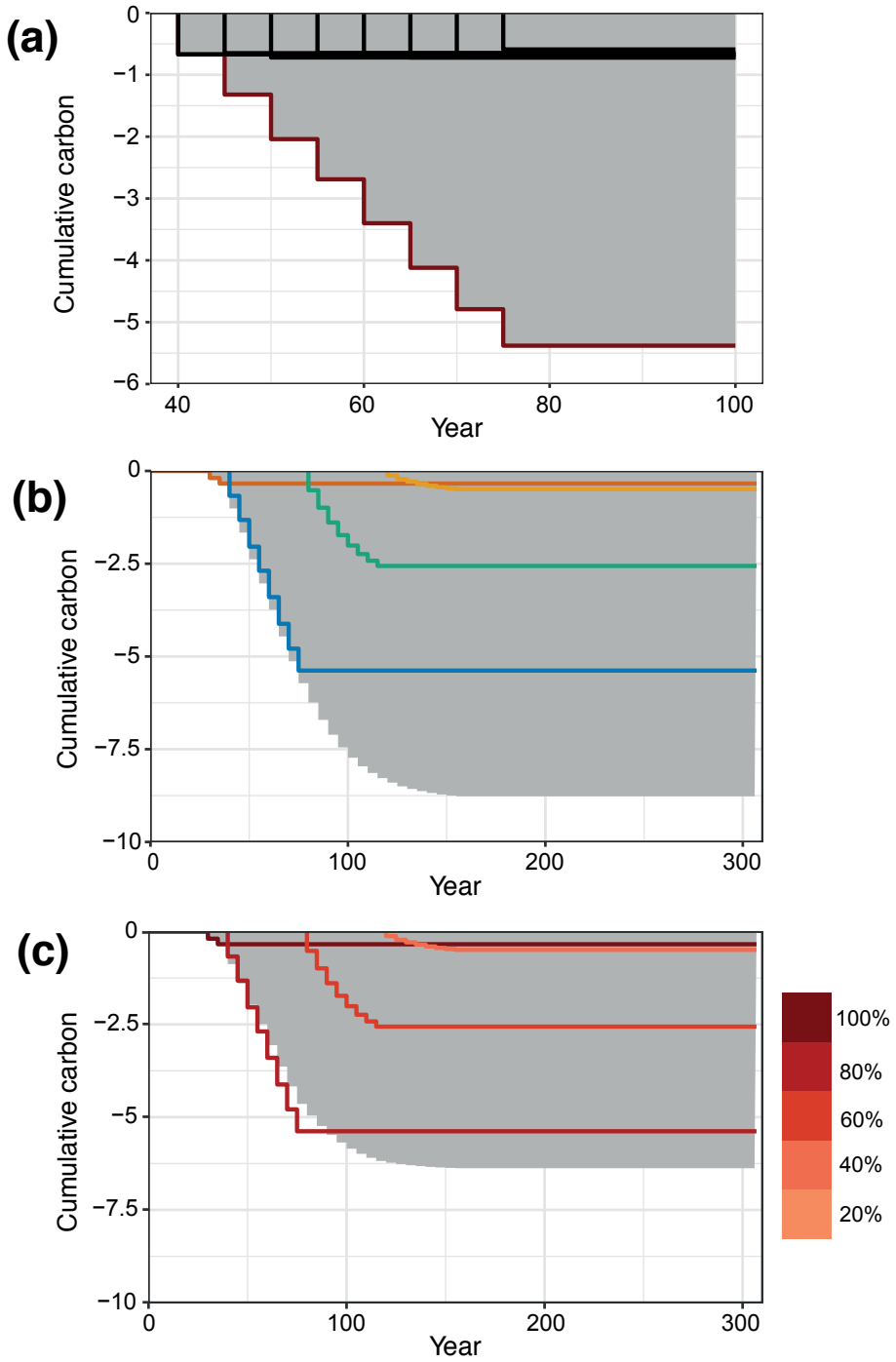
Appendix figure A.2: (a) Carbon is removed from the stand every 40 years. This decays over time (exact rates of decay are according to the expected residency and decay periods of different types of wood products). Each felling event is indicated by a different coloured line. The grey shaded area shows the total cumulative carbon that is in a decay phase from all felling events combined. (b) Only 20% of the standing carbon is removed from each felling event, so each decay event is multiplied by 20%. The grey shaded area shows the corresponding total cumulative carbon that is in a decay phase from all felling events combined. The lines for each period are the same as Fig. b, but their colour indicates the percentage by which they are multiplied.

Decay from thinning

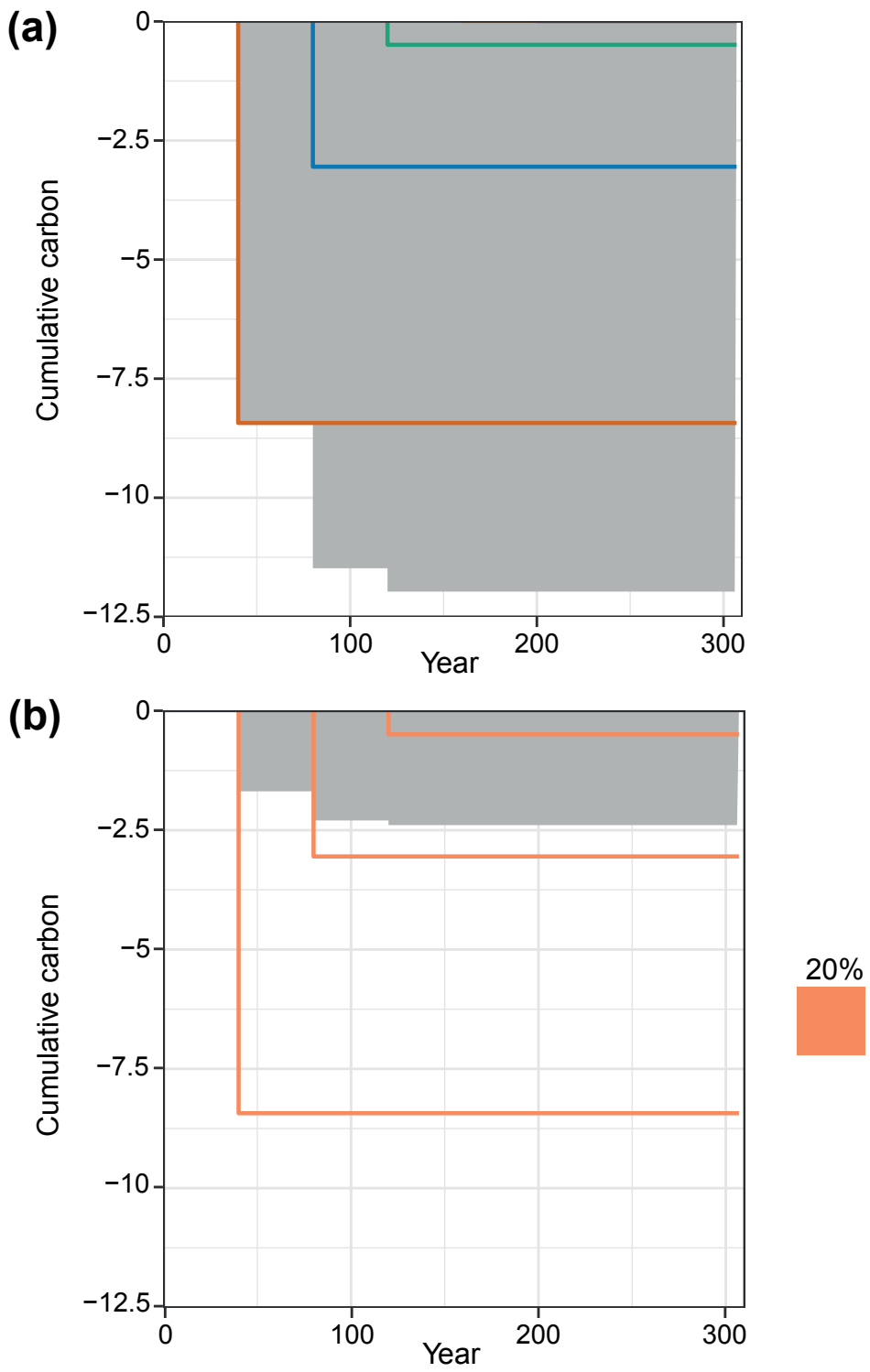


Appendix figure A.3: (a) Carbon is removed every 5 years in thinning operations. The black lines indicate the cumulative decay of carbon removed from each thinning event in the period of years 40-80. The grey shaded area and blue line shows the total cumulative carbon that is in a decay phase from all the thinning events in this period combined. (b) Each coloured line indicates the cumulative carbon decay from thinning events of the different periods [the blue line is the same as (a)]. The grey shaded area shows the total cumulative carbon that is in a decay phase from all the thinning events over all periods. (c) As 20% of the stand is removed by felling every 40 years, the total carbon removed in thinning events decreases accordingly. The grey shaded area shows the total cumulative carbon, taking into account the decreases in carbon removed in thinning events for each 40-year period. The lines for each period are the same as (b), but their shading indicates the proportion of the original stand left in each period, and therefore the percentage by which to multiply the carbon removal and subsequent decay.

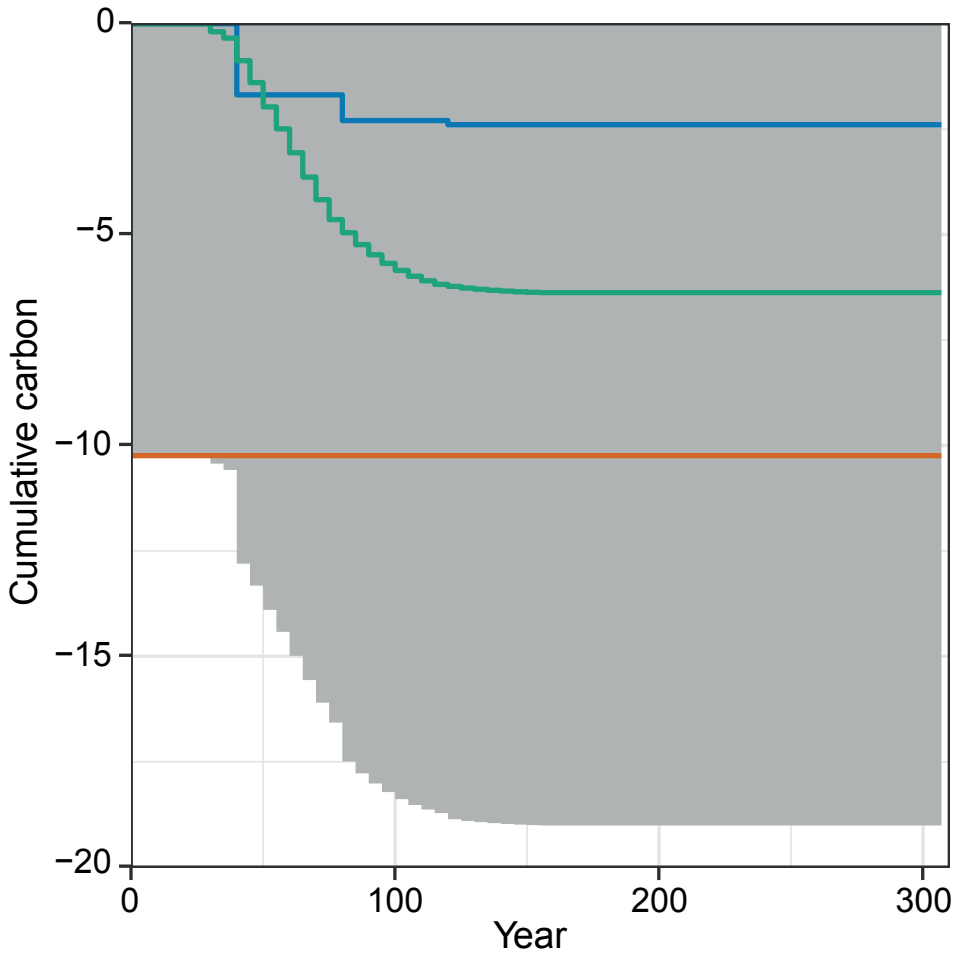
Emissions



Appendix figure A.4: Management emissions from thinning operations every 5 years. (a) The black lines indicate the cumulative management emissions from each 5-yearly thinning event in the period of years 40-80. The grey shaded area and dark red line shows the total cumulative management emissions from all the thinning operations in this period. (b) Each coloured line indicates the cumulative management emissions from thinning events in all the different periods [the blue line is the same as the dark red line in (a)]. The grey shaded area shows the total cumulative emissions from all the thinning operations over all periods. (c) As 20% of the stand is removed by felling every 40 years, the thinning events and emissions from operations are scaled accordingly. The grey shaded area shows the total cumulative emissions taking this into account. The lines for each period are the same as (b), but their shading indicates the proportion of the original stand left in each period, and therefore the percentage by which to multiply the emissions.

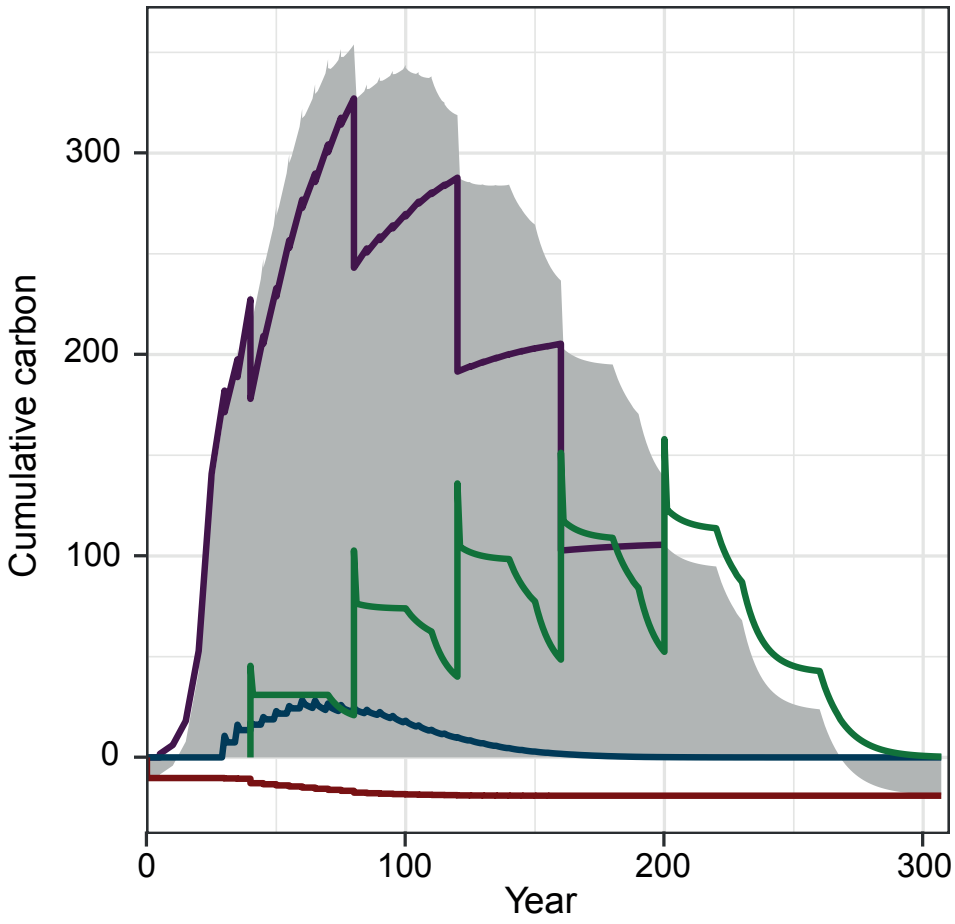


Appendix figure A.5: Felling emissions from felling events every 40 years. (a) Each coloured line indicates the cumulative emissions from each felling event. Felling emissions are calculated as the final management emission given in the lookup tables at year 200, minus the emissions from management operations up to that point (as stated in the Woodland Carbon Code guidance), which explains why this proxy for clearfell emissions decreases through time. The grey shaded area shows the total cumulative emissions from all the felling operations. (b) Only 20% of the stand is felled every 40 years, so the emissions from felling operations are scaled accordingly. The grey shaded area shows the total cumulative emissions, taking into account this proportion. The lines for each period are the same as (a), but their colour indicates the percentage by which they are multiplied.



Appendix figure A.6: Total emissions. The green line indicates the cumulative management emissions from thinning [grey shaded area in Appendix figure A.4c)]. The blue line indicates the cumulative felling emissions [grey shaded area in Appendix figure A.5b]. The orange line indicates the cumulative emissions resulting from the establishment of the stand (year 0). The grey shaded area shows the total cumulative emissions from all categories.

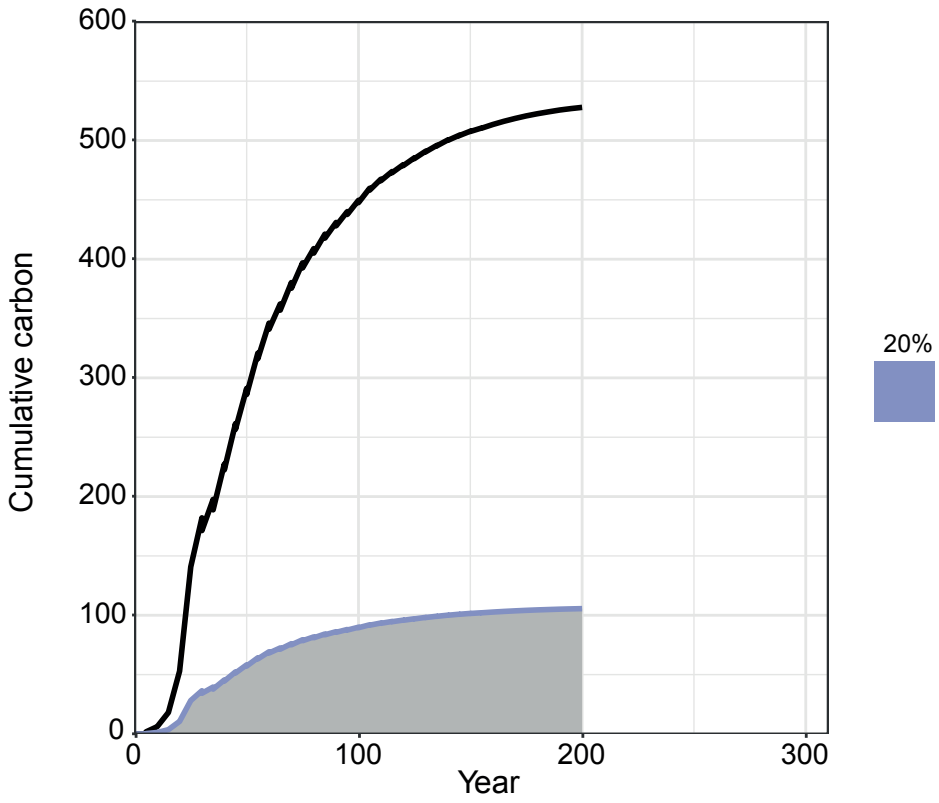
Total cumulative carbon



Appendix figure A.7: The purple line indicates the cumulative carbon in standing biomass (grey shaded area in Appendix figure A.1). The green line indicates the cumulative carbon that is in a decay phase from felling events [grey shaded area in Appendix figure A.2b). The blue line indicates the cumulative carbon that is in a decay phase from thinning events [grey shaded area in Appendix figure A.3c]. The dark red line indicates the total cumulative emissions (grey shaded area in Appendix figure A.6). The grey shaded area shows the total cumulative carbon sequestered over the full life-cycle of the first stand in a continuous-cover system.

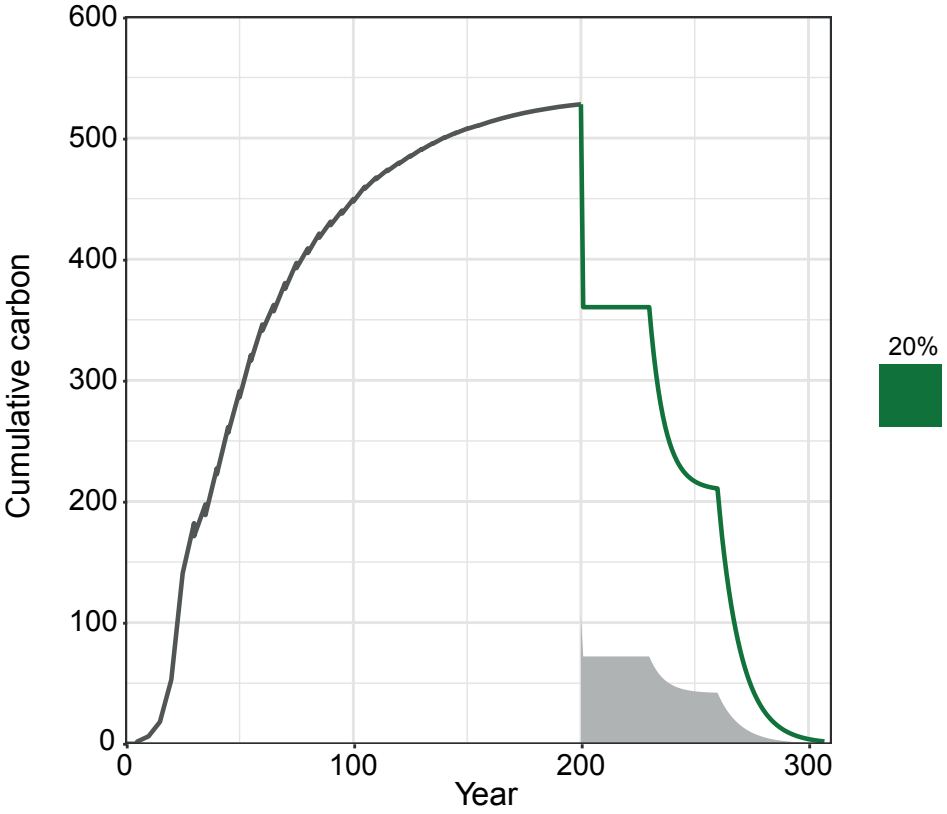
Secondary stands

Standing biomass



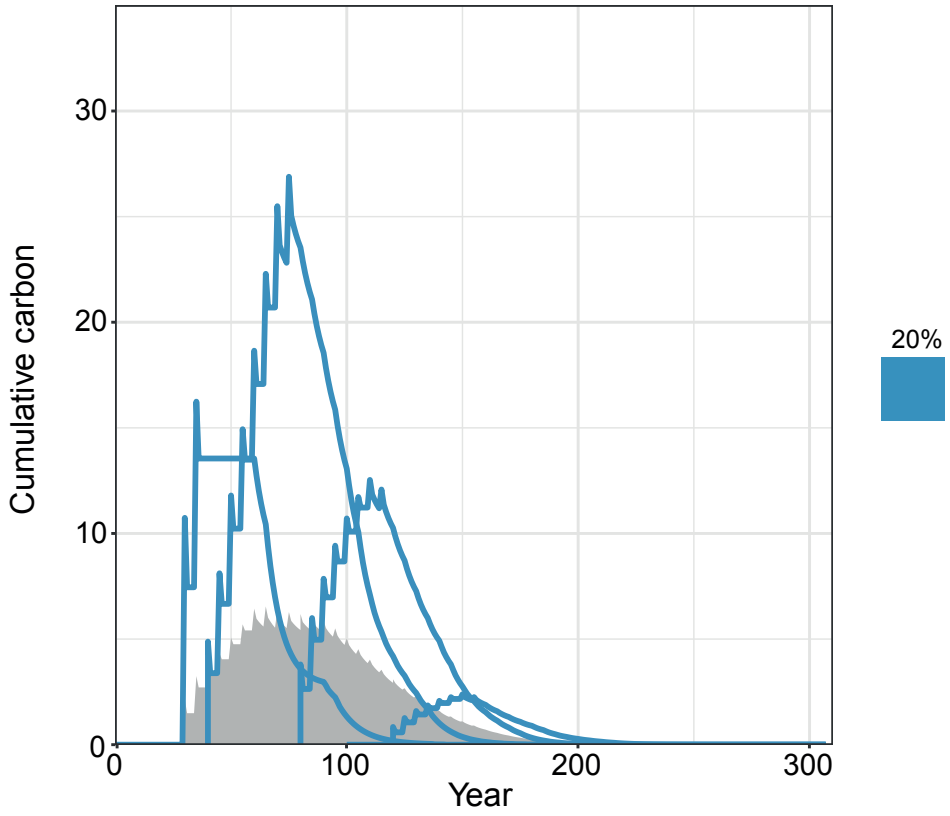
Appendix figure A.8: The black line indicates the carbon accumulated in standing biomass (as for Appendix figure A.1). Secondary stands correspond to 20% of the total area throughout their lifetime, so the total potential carbon sequestration is multiplied by 20%. The grey shaded area shows the overall carbon sequestered in standing biomass over time.

Decay from felling



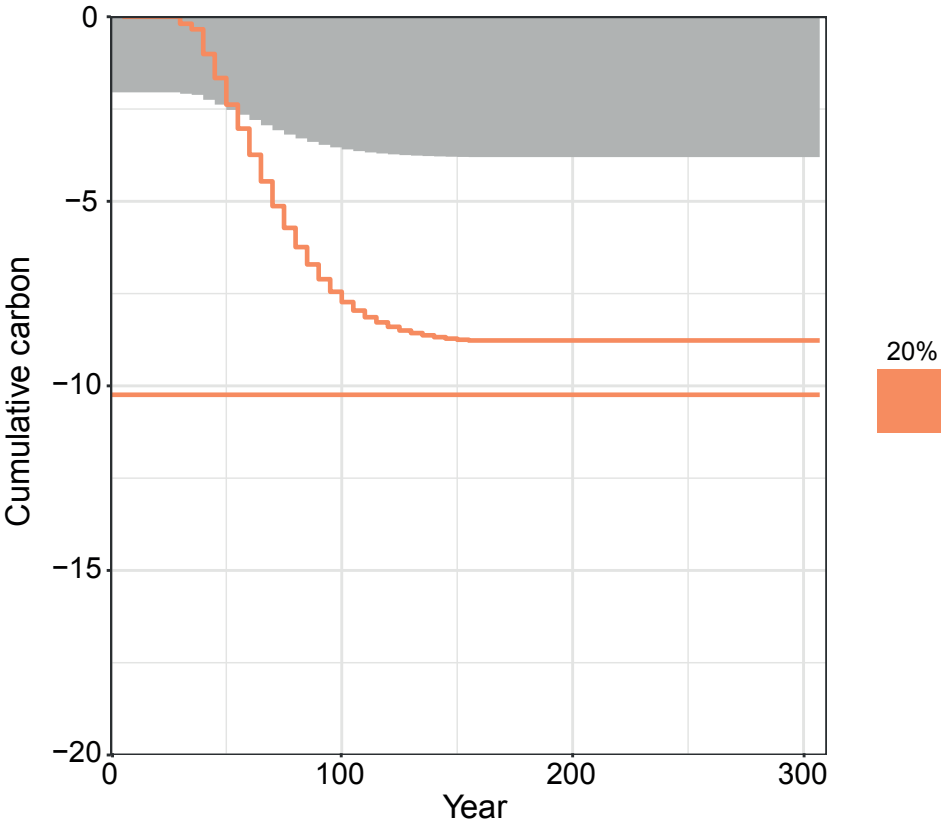
Appendix figure A.9: After 200 years, this stand is felled. The green line indicates the decay of the carbon removed (exact rates of decay are according to the expected residency and decay periods of different types of wood products). This is multiplied by 20% (as secondary stands correspond to 20% of the total area throughout their lifetime). The grey shaded area shows the total cumulative carbon decay from the felling event.

Decay from thinning



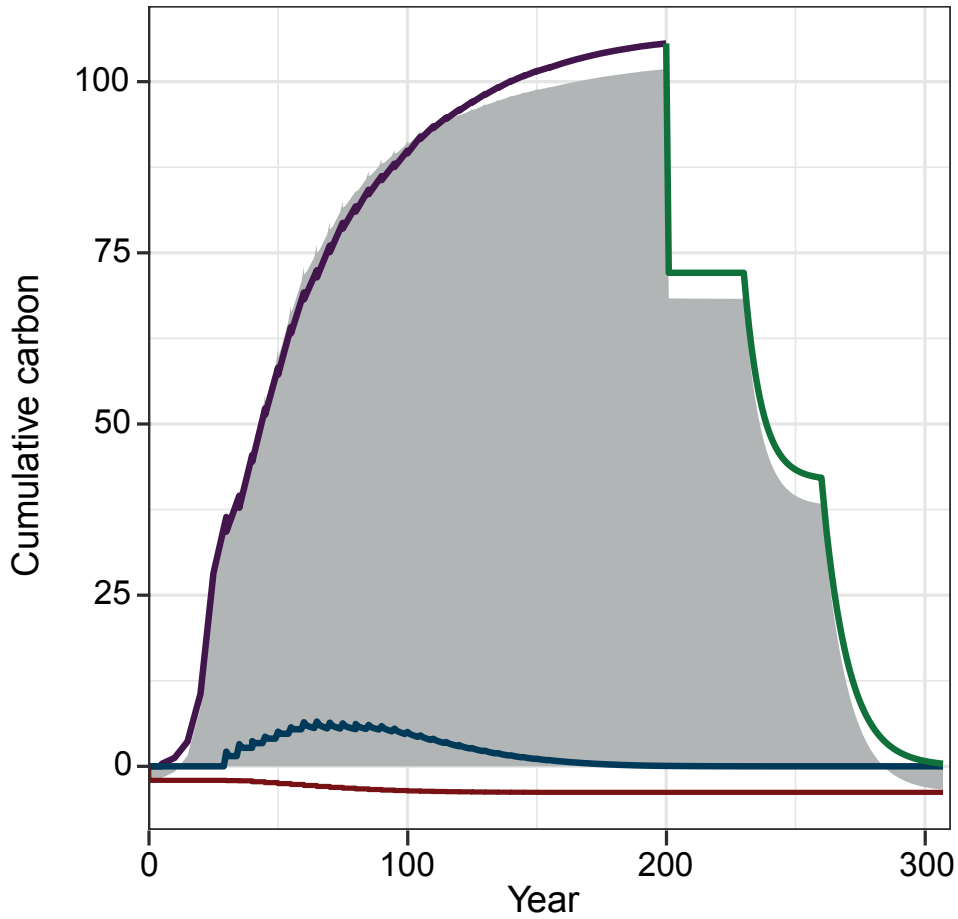
Appendix figure A.10: Blues lines show the cumulative carbon from the thinning events of different 40-year periods [as for Appendix figure A.3b and c]. This is multiplied by 20% (as secondary stands correspond to 20% of the total area throughout their lifetime). The grey shaded area shows the total cumulative carbon decay from the thinning events.

Emissions



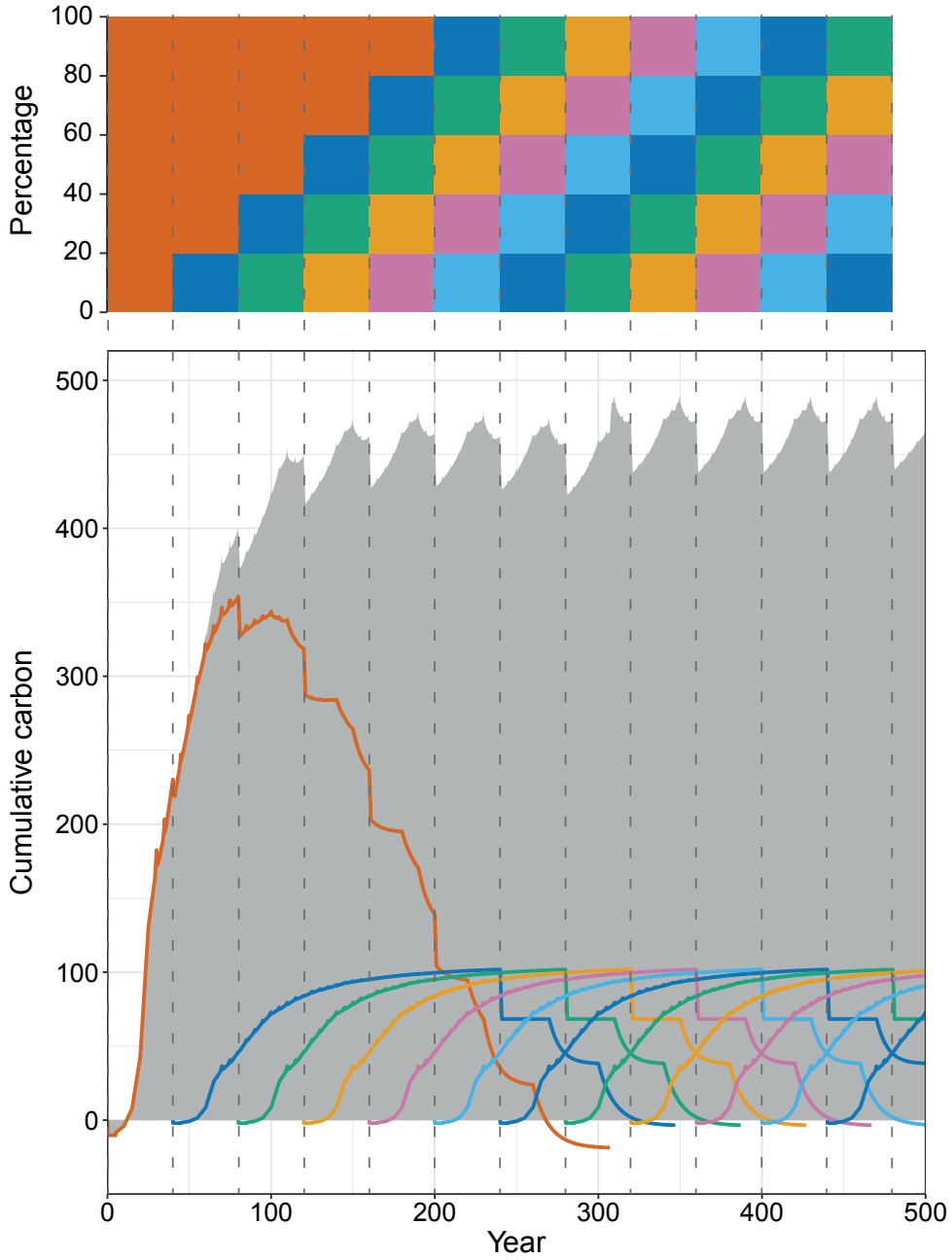
Appendix figure A.11: The lines indicate the cumulative management emissions from thinning and stand establishment (as for Appendix figure A.6). There is no emissions calculated for felling at year 200 (as the method of calculating clearfell emissions is to subtract total management emissions to date from the total management emissions at year 200). These cumulative emissions are multiplied by 20% (as secondary stands correspond to 20% of the total area throughout their lifetime). The grey shaded area shows the total cumulative emissions.

Total cumulative carbon



Appendix figure A.12: The purple line indicates the cumulative carbon in standing biomass (grey shaded area in Appendix figure A.8). The green line indicates the cumulative carbon that is in a decay phase from felling events (grey shaded area in Appendix figure A.9). The blue line indicates the cumulative carbon that is in a decay phase from thinning events (grey shaded area in Appendix figure A.10). The dark red line indicates the total cumulative emissions (grey shaded area in Appendix figure A.11). The grey shaded area shows the total cumulative carbon sequestered over the full life-cycle of secondary stands in a continuous-cover system.

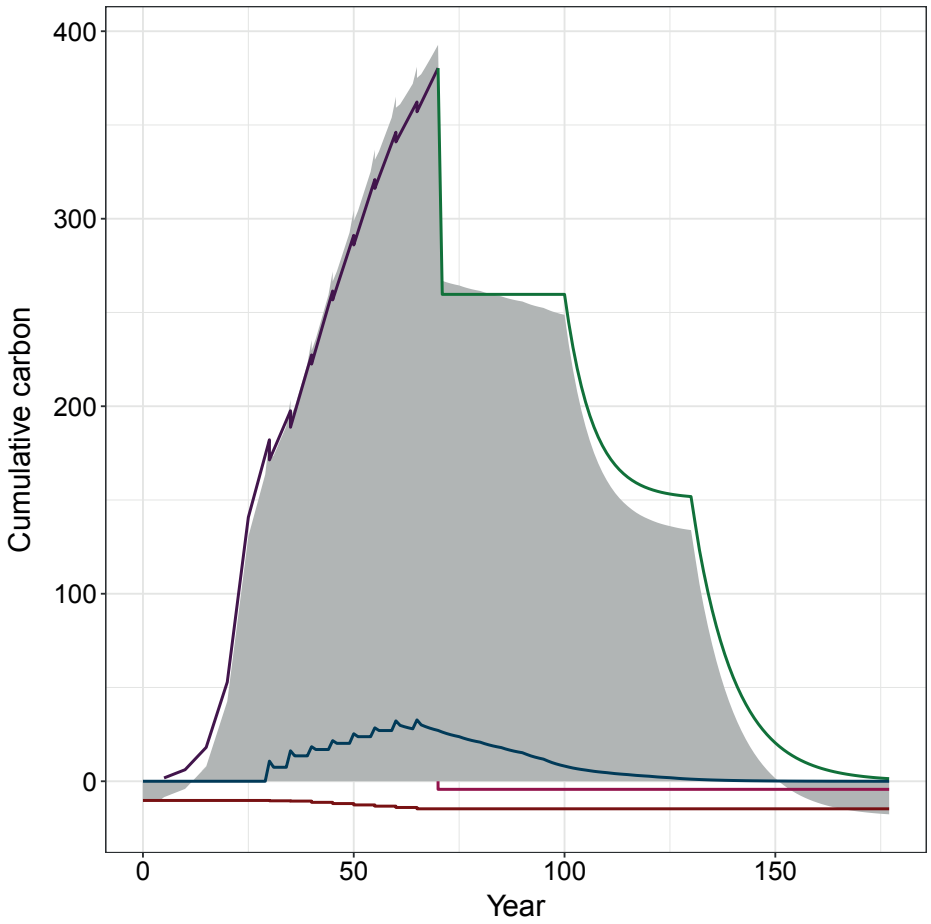
Overall continuous-cover life-cycle



Appendix figure A.13: The lower panel shows the cumulative carbon sequestered over the full life-cycles of different stands as they are present in the system. The orange line indicates the life-cycle of the first stand (the grey shaded area in Appendix figure A.7). The dark blue, green, yellow, pink and light blue lines indicate subsequent life-cycles of secondary stands. The grey shaded area shows the total cumulative carbon sequestration. The upper panel shows the percentage composition and age classes of different stands within the overall area. Initially, the first (orange) stand covers 100% of the area. 20% of the largest trees are removed every 40 years; for the first 200 years these are from the first (orange) stand. Regeneration in these gaps leads to the growth of new stands, which constitute 20% of the total area over their lifetime. After 200 years, the overall area constitutes an even mix of age classes. Each line in the lower panel extends beyond its corresponding block(s) in the upper panel, as the upper panel shows the percentages and age classes of living components in the overall area, whereas the lower panel shows the full carbon life-cycle of each stand (which extends beyond the point at which it is no longer living through carbon decay in wood products).

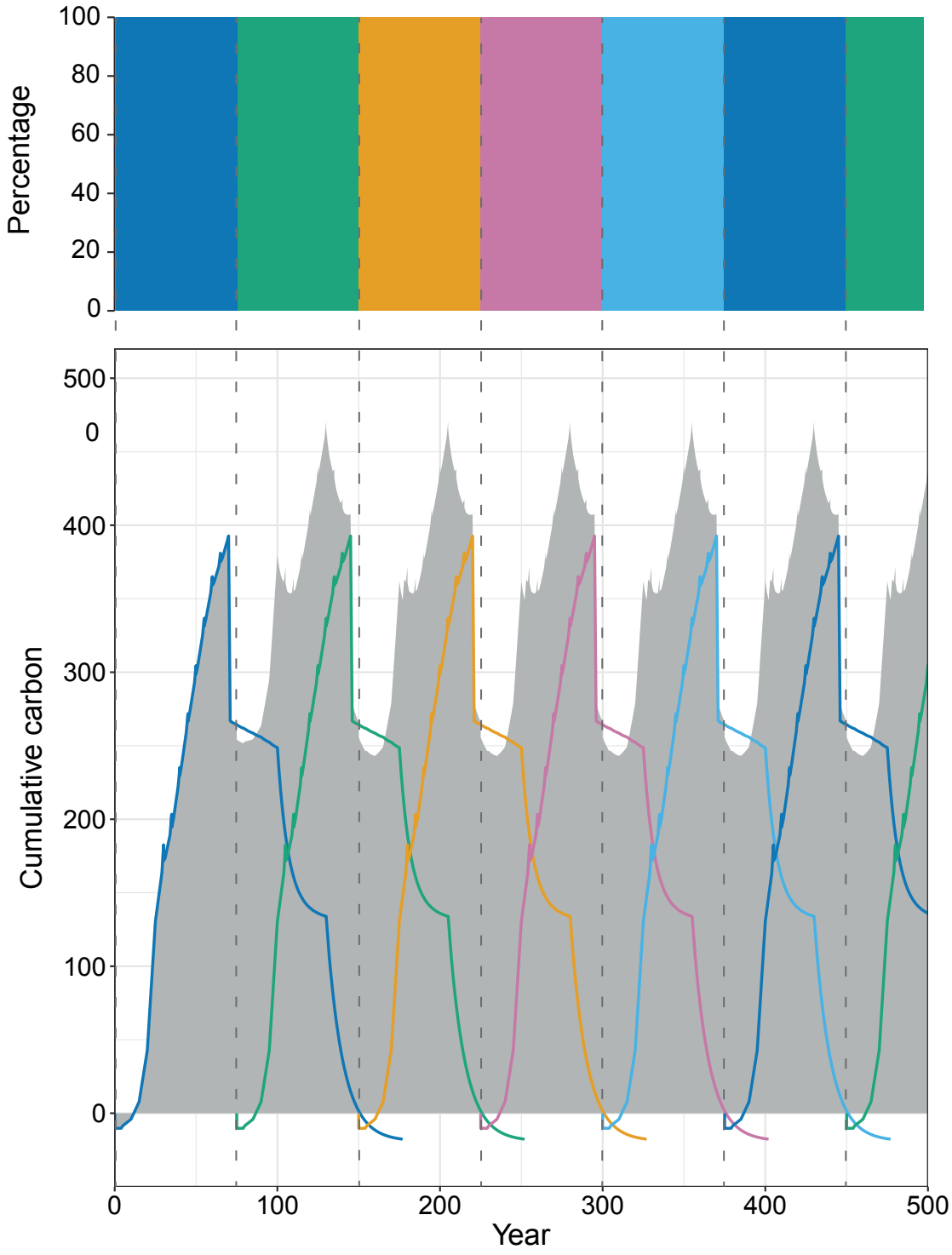
Clearfell

Total cumulative carbon for clearfell stands



Appendix figure A.14: The purple line indicates the cumulative carbon in standing biomass (up to year 70, when it is felled). The green line indicates the cumulative carbon decay phase from felling. The blue line indicates the cumulative carbon decay from thinning events. The dark red line indicates the total cumulative management and establishment emissions. The pink line indicates the cumulative emissions from felling at year 70. The grey shaded area shows the total cumulative carbon sequestered over the full life-cycle of the stand.

Overall clearfell life-cycle



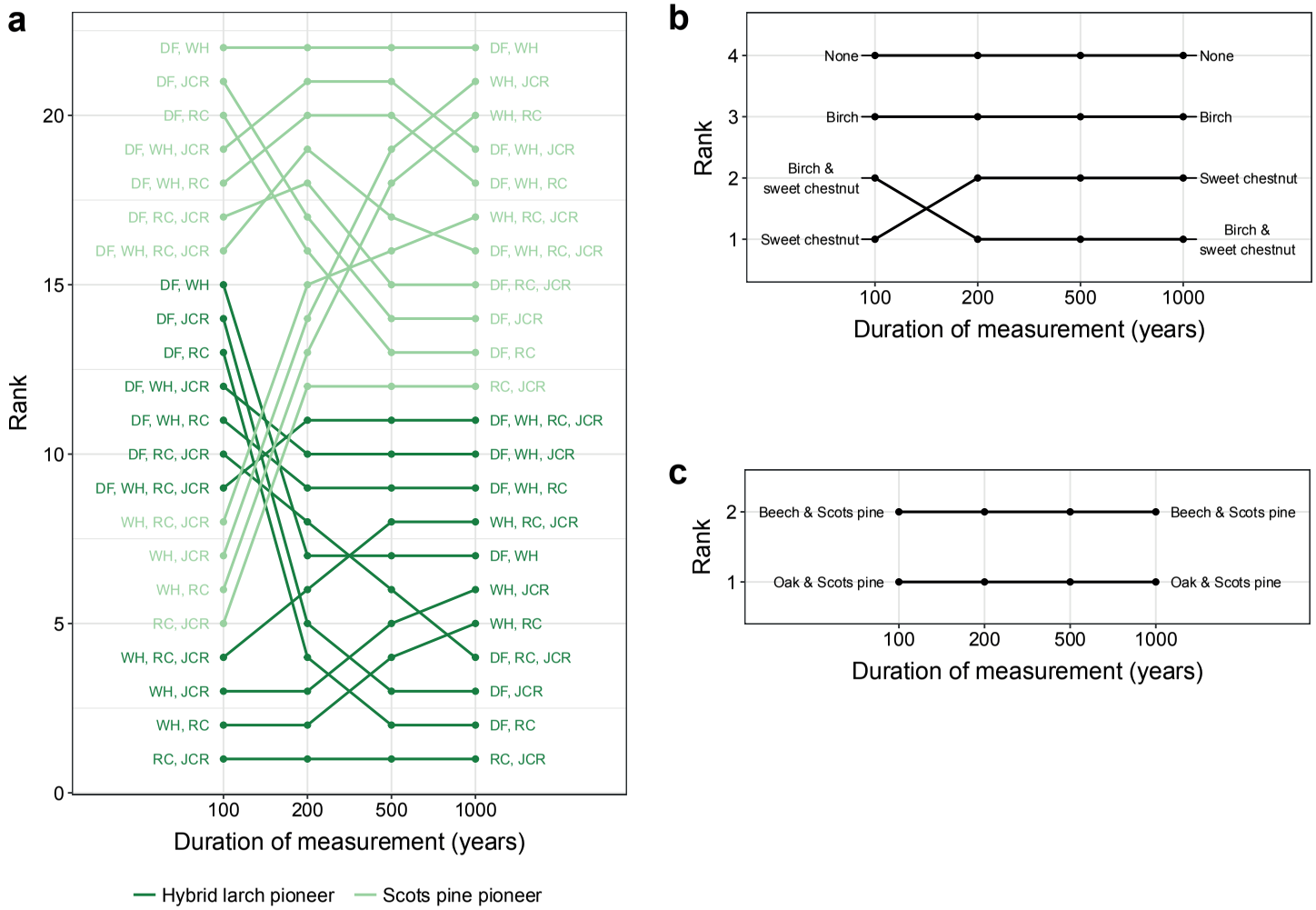
Appendix figure A.15: The lower panel shows the cumulative carbon sequestered over the full life-cycles of different stands as they are present in the system. The upper panel shows the percentage composition and age classes of different stands within the overall area. Each line in the lower panel extends beyond its corresponding block(s) in the upper panel, as the upper panel shows the percentages and age classes of living components in the overall area, whereas the lower panel shows the full carbon life-cycle of each stand (which extends beyond the point at which it is no longer living through carbon decay in wood products).

Appendix table A.3: Full results for carbon indicator values ($tCO_2\ ha^{-1}\ year^{-1}$), calculated for each of the management options. The different columns indicate values calculated for either continuous-cover or clearfell options, and over the four different time periods: 100, 200, 500 and 1000 years.

Description	Species		Continuous-cover				Clearfell			
			100	200	500	1000	100	200	500	1000
Conifer monoculture	Corsican pine		292.37	359.79	385.07	397.14	260.61	324.77	356.12	366.54
	Douglas fir		333.67	422.80	470.62	489.97	301.88	390.88	434.75	447.81
	Hybrid larch		221.50	256.72	259.31	263.48	200.81	250.85	279.93	287.14
	Japanese larch		233.06	270.87	273.90	278.20	211.56	264.80	295.93	303.68
	Scots pine		240.61	348.42	423.90	452.07	211.62	283.75	322.35	334.46
	Serbian spruce		170.16	260.65	323.98	348.25	157.63	204.56	238.77	246.93
	Western hemlock		347.03	498.19	611.24	654.25	319.41	409.18	468.68	483.24
	Western red cedar		309.48	443.14	528.00	560.13	288.01	374.76	434.82	449.67
	Other conifer		268.65	371.06	435.72	460.75	242.89	315.04	359.84	371.78
Conifer mixture	Scots pine pioneer	Douglas fir	287.14	385.61	447.26	471.02	256.75	337.31	378.55	391.14
		Western hemlock	255.26	377.70	468.21	502.15	237.52	307.96	357.04	369.03
		Western red cedar	255.24	368.10	440.68	468.15	238.33	310.78	361.58	374.11
		Japanese cedar	255.24	368.10	440.68	468.15	238.33	310.78	361.58	374.11
		Serbian spruce	221.90	327.96	402.12	430.09	207.06	270.33	314.03	324.91
	Hybrid larch pioneer	Douglas fir	277.58	339.76	364.96	376.72	253.51	321.82	364.17	374.62
		Western hemlock	245.70	331.86	385.91	407.85	225.20	285.92	325.55	335.15
		Western red cedar	245.68	322.25	358.38	373.85	226.01	288.74	330.09	340.23
		Japanese cedar	245.68	322.25	358.38	373.85	226.01	288.74	330.09	340.23
		Serbian spruce	212.35	282.12	319.82	335.79	194.74	248.29	282.53	291.03
	Underplanting Scots pine pioneer	Douglas fir	238.10	360.03	437.29	466.03	214.65	266.05	296.55	308.37
		Western hemlock	210.43	348.71	456.64	496.36	198.31	240.20	265.60	273.83
		Western red cedar	209.97	342.49	430.66	463.14	198.02	242.25	269.12	277.91
		Japanese cedar	209.97	342.49	430.66	463.14	198.02	242.25	269.12	277.91

		Serbian spruce	186.99	306.48	393.60	425.83	174.14	209.97	231.78	238.79
	Underplanting hybrid larch pioneer	Douglas fir	228.55	314.19	354.99	371.74	210.02	260.65	292.46	303.74
		Western hemlock	200.87	302.86	374.34	402.07	193.68	235.92	261.53	269.70
		Western red cedar	200.41	296.65	348.36	368.85	193.40	237.97	265.04	273.78
		Japanese cedar	200.41	296.65	348.36	368.85	193.40	237.97	265.04	273.78
		Serbian spruce	177.44	260.63	311.30	331.53	169.52	205.69	227.70	234.66
	Scots pine pioneer	Douglas fir, western hemlock	281.39	392.74	469.01	498.09	NA	NA	NA	NA
		Douglas fir, western red cedar	281.38	386.33	450.66	475.42	NA	NA	NA	NA
		Douglas fir, Japanese cedar	281.38	386.33	450.66	475.42	NA	NA	NA	NA
		Western hemlock, western red cedar	260.13	381.06	464.62	496.18	NA	NA	NA	NA
		Western hemlock, Japanese cedar	260.13	381.06	464.62	496.18	NA	NA	NA	NA
		Western red cedar, Japanese cedar	260.12	374.66	446.27	473.51	NA	NA	NA	NA
		Douglas fir, western hemlock, western red cedar	278.51	391.50	466.12	494.62	NA	NA	NA	NA
		Douglas fir, western hemlock, Japanese cedar	278.51	391.50	466.12	494.62	NA	NA	NA	NA
		Douglas fir, western red cedar, Japanese cedar	278.50	386.70	452.35	477.63	NA	NA	NA	NA
		Western hemlock, western red cedar, Japanese cedar	262.56	382.74	462.83	493.19	NA	NA	NA	NA
		Douglas fir, western hemlock, western red cedar, Japanese cedar	276.78	390.75	464.39	492.55	NA	NA	NA	NA
	Hybrid larch pioneer	Douglas fir, western hemlock	275.02	362.17	414.15	435.22	NA	NA	NA	NA
		Douglas fir, western red cedar	275.01	355.77	395.79	412.56	NA	NA	NA	NA
		Douglas fir, Japanese cedar	275.01	355.77	395.79	412.56	NA	NA	NA	NA

		Western hemlock, western red cedar	253.76	350.50	409.76	433.31	NA	NA	NA	NA
		Western hemlock, Japanese cedar	253.76	350.50	409.76	433.31	NA	NA	NA	NA
		Western red cedar, Japanese cedar	253.75	344.09	391.40	410.65	NA	NA	NA	NA
		Douglas fir, western hemlock, western red cedar	273.73	368.57	424.97	447.48	NA	NA	NA	NA
		Douglas fir, western hemlock, Japanese cedar	273.73	368.57	424.97	447.48	NA	NA	NA	NA
		Douglas fir, western red cedar, Japanese cedar	273.73	363.77	411.21	430.48	NA	NA	NA	NA
		Western hemlock, western red cedar, Japanese cedar	257.78	359.82	421.68	446.04	NA	NA	NA	NA
		Douglas fir, western hemlock, western red cedar, Japanese cedar	272.96	372.42	431.47	454.83	NA	NA	NA	NA
Broadleaved monoculture	Birch		182.54	248.44	290.33	307.04	NA	NA	NA	NA
	Eucalyptus		295.28	361.01	395.79	411.31	NA	NA	NA	NA
	Sweet chestnut		150.86	229.63	281.15	301.24	NA	NA	NA	NA
	Other broadleaved		180.51	251.61	296.93	314.88	NA	NA	NA	NA
Broadleaved mixture	Birch pioneer	Beech, oak, Sycamore	189.85	262.62	308.62	326.87	NA	NA	NA	NA
	Sweet chestnut pioneer	Beech, oak, Sycamore	181.93	257.92	306.32	325.41	NA	NA	NA	NA
	No pioneer	Beech, oak, Sycamore	192.28	267.35	314.71	333.47	NA	NA	NA	NA
	Birch & sweet chestnut pioneer	Beech, oak, Sycamore	182.05	256.02	303.12	321.74	NA	NA	NA	NA
Conifer and broadleaved mixture	Scots pine & beech		226.19	326.80	393.69	419.20	NA	NA	NA	NA
	Scots pine & oak		211.58	298.43	357.12	379.55	NA	NA	NA	NA



Appendix figure A.16: The relative ranks taken from the carbon indicator values of different management options according to duration of measurement. (a) Conifer mixtures with more than two species. Colour indicates the pioneer species. Additional species are given as symbols for clarity, as follows. WH: western hemlock, DF: Douglas fir, JCR: Japanese cedar, RC: western red cedar, OMS: Serbian spruce. (b) Broadleaved mixtures. The species label indicates the pioneer species in addition to the mixture of beech, oak and sycamore. (c) Conifer and broadleaved mixtures.

Appendix table B.1: Full information on plots visited.

Category	Species composition (year of planting)	Number of species	Compartment number	Plot no.	Soil information (from Corbett map, 1973)		Area	Average GPS point of sub-plots	
					Soil series	Type of soil		Longitude	Latitude
Conifer monoculture	100% Scots pine (1960)	1	2974 B	7	Methwold	Calcareous	2.65	580928.3	288735
Conifer monoculture	100% Corsican pine (1965)	1	2922 B	8	Santon	Acidic	4.22	580956.7	290745
Conifer monoculture	100% Scots pine (1927)	1	3143 A	9	Worlington	Acidic	5.06	581648.3	291781.7
Conifer monoculture	100% Douglas fir (1928)	1	3523 A	11	Methwold	Calcareous	8.82	580990	287222.5
Conifer monoculture	100% hybrid larch (1999)	1	3409 C	12	Worlington	Acidic	3.96	578502.5	282080
Conifer monoculture	100% Weymouth pine (1964)	1	4501 B	22	Worlington	Acidic	0.53	580797.5	276760
Conifer mixture	42% Grand fir (1966), 40% Corsican pine (1966), 18% Scots pine (1929)	3	2559 A	18	Methwold	Calcareous	5.65	576203.3	291816.7
Conifer mixture	48% Scots pine (1970), 48% Corsican pine (1970), 4% mixed conifers (1926)	3+	3844 A	20	Methwold	Calcareous	9.2	583660	283445
Conifer mixture	40% Corsican pine (1911), 40% Scots pine (1911), 20% Douglas fir (1911)	3	3938 B	21	Methwold	Calcareous	2.66	588717.5	287752.5
Conifer mixture	50% Scots pine (1927), 30% European larch (1927), 20% Douglas fir (1927)	3	2161 B	50	Worlington	Acidic	2.66	579562.5	306040
Conifer mixture	45% Scots pine (1995), 35% Corsican pine (1995), 10% European silver fir (2014), 10% Douglas fir (2014)	4	3793 B	51	Worlington	Acidic	4.55	581785	282435
Conifer mixture	60% Douglas fir (1932, 1980), 40% Grand fir (1932, 1980)	2	2918 A	52	Santon	Acidic	5.49	581130	290962
Broadleaved monoculture	100% sweet chestnut (1979)	1	2716 A	1	Methwold	Calcareous	4.56	579675	293280
Broadleaved monoculture	100% eucalyptus (1980)	1	2934 A	3	Methwold	Calcareous	2.76	580018.8	290111.3
Broadleaved monoculture	100% oak (1933)	1	4207 B	4	Worlington	Acidic	2.76	595350	283942.5
Broadleaved monoculture	100% beech (1932)	1	4282 B	5	Worlington	Acidic	4.55	595650	283410
Broadleaved monoculture	100% birch (1953)	1	4766 C	6	Worlington	Acidic	2.61	583887.5	273995
Broadleaved mixture	50% beech (1949), 20% ash (1949), 25% mixed broadleaves (1900, 1985), 5% oak (1850)	5+	2799 B	13	Methwold	Calcareous	6.33	579495	289457.5
Broadleaved mixture	51% beech (1939), 29% Sycamore (1900), 20% oak (1900)	3	3542 B	14	Methwold	Calcareous	3.86	582744	286330
Broadleaved mixture	50% mixed broadleaves (1975), 25% lime (1966), 25% Sycamore (1966)	3+	4257 A	15	Worlington	Acidic	3.21	597100	283902.5
Broadleaved mixture	49% oak (1970), 33% beech (1960), 11% ash (1970), 7% Sycamore (1970)	4	4264 A	16	Methwold	Calcareous	5.92	598175	284430

Broadleaved mixture	80% beech (1951, 1960), 11% birch (1951), 9% Sycamore (1951)	3+	4624 B	17	Worlington	Acidic	3.43	581375	272940
Mixed (primary conifer)	53% Scots pine (1932), 26% mixed broadleaves (1932), 21% ash (1932)	3+	2922 A	28	Santon	Acidic	9.38	580764	290822
Mixed (primary conifer)	60% Scots pine (1930), 30% Sycamore (1985), 10% sweet chestnut (1975)	3	3141 B	29	Worlington	Acidic	4.72	581530	291937.5
Mixed (primary conifer)	50% European Larch (1926), 30% Scots pine (1926), 20% beech (1926)	3	3843 A	30	Methwold	Calcareous	16.55	583777.5	283507.5
Mixed (primary conifer)	50% Corsican pine (1988), 45% Scots pine (1988), 5% birch (1988)	3	3923 A	31	Freckenham	Acidic	13.87	588940	288252.5
Mixed (primary conifer)	49% Scots pine (1938), 25% oak (1938), 20% beech (1938), 6% sweet chestnut (1938)	4	4228 A	32	Methwold	Calcareous	8.83	597257.5	284752.5
Mixed (primary broad)	40% beech (1907, 1950), 29% European larch (1907), 20% Scots pine (1907), 11% Douglas fir (1907)	4	3703 A	23	Worlington	Acidic	5.29	579165	284820
Mixed (primary broad)	54% beech (1948), 30% Scots pine (1948), 10% oak (1948), 6% birch (1948)	4	2997 A	24	Methwold	Calcareous	7.14	580524	288210
Mixed (primary broad)	40% sweet chestnut (1975), 30% Scots pine (1927), 15% mixed broadleaves (1975), 15% Sycamore (1990)	4+	3140 C	25	Worlington	Acidic	2.76	581757.5	291905
Mixed (primary broad)	50% oak (1934), 40% Scots pine (1934), 10% beech (1934)	3	4223 B	26	Methwold	Calcareous	3.61	597245	285055
Mixed (primary broad)	60% beech (1910), 25% Corsican pine (1955), 15% Scots pine (1955)	3	4775 B	27	Methwold	Calcareous	3.95	583075	274050
Open (cleared)			2514 A	36	Methwold	Calcareous	17.72	577212.5	294127.5
Open (cleared)			2590 A	37	Freckenham	Acidic	13.28	575225	289282.5
Open (cleared)			2711 A	38	Methwold	Calcareous	10.18	578322.5	293305
Open (cleared)			3005 B	40	Freckenham	Acidic	4.42	582170	287920
Open (cleared)			4292 A	41	Methwold	Calcareous	8.21	598240	283240
Heathland			2518 A	33	Methwold	Calcareous	10.3	577465	294125
Heathland			4523 B	34	Worlington	Acidic	2.36	580838	275722
Heathland			Weeting Heath	42	Methwold	Calcareous		575810	288102.5
Heathland			East Wretham	45	Freckenham	Acidic		591544	288162
Heathland			Thetford Heath	44	Methwold	Calcareous		584905	279600

Appendix table B.2: Full linear models. Each row represents a different linear model.

Dependent variable	Management options included	Soil layers included	Historical soil type included
Total carbon concentration	All	All	All
	All	Mineral soils samples only	All
Total nitrogen concentration	All	All	All
	All	Mineral soils samples only	All
C:N ratio	All	All	All
	All	Mineral soils samples only	All
	All	Organic soils samples only	All
Thickness of F and litter layers	All	All	All
Layer carbon stock	All	All	All
Total plot carbon stock	All	All	All
	All	Mineral soil samples only	All
Layer nitrogen stock	All	All	All
Total plot nitrogen stock	All	All	All
	All	Mineral soil samples only	All

Appendix table B.3: Mean layer stocks for carbon and nitrogen. Means are calculated across all plots in tonnes per hectare. Numbers in brackets are the standard deviation.

Carbon

Depth	Conifer monoculture	Conifer mixture	Mixture (primary conifer)	Mixture (primary broadleaved)	Broadleaved monoculture	Broadleaved mixture	Open (cleared)	Heathland
Litter layer	2.24 (1.69)	2.19 (0.85)	2.58 (1.53)	3.05 (2.35)	2.06 (1.8)	1.77 (1)	0.17 (NA)	NA
Grass	NA	NA	NA	NA	NA	NA	0.19 (0.13)	0.18 (0.07)
F layer	34.92 (27.67)	42.9 (31.27)	34.09 (33.89)	21.49 (16.1)	9.6 (11.74)	9.82 (11.14)	NA	NA
0-5cm depth	16.84 (4.84)	9.83 (3.47)	17.26 (5.44)	18.31 (4.7)	12.84 (5.67)	12.26 (5.1)	23.41 (13.94)	14.54 (5.67)
5-10cm depth	9.46 (2.86)	11.89 (8.17)	10.28 (4.06)	9.95 (4.96)	6.61 (2.05)	7.93 (3.19)	10.25 (5.17)	11.68 (2.03)
10-20cm depth	11.42 (2.27)	16.78 (8.84)	13.16 (5.98)	16.94 (13.83)	9.64 (3.89)	10.26 (5.86)	13.46 (6.51)	16.19 (6.95)
Organic layers total	37.16 (28.94)	45.09 (30.83)	36.66 (34.46)	24.54 (16.76)	11.67 (13.30)	11.59 (11.96)	0.24 (0.21)	0.18 (0.07)
Mineral layers total	37.72 (7.54)	38.50 (10.85)	40.71 (14.83)	45.19 (20.19)	29.09 (6.80)	30.45 (13.70)	47.12 (22.18)	42.42 (13.51)
All layers total	74.87 (25.56)	83.60 (34.29)	77.38 (37.30)	69.74 (30.59)	40.76 (18.02)	42.04 (19.60)	47.31 (22.13)	42.60 (13.50)

Nitrogen

Depth	Conifer monoculture	Conifer mixture	Mixture (primary conifer)	Mixture (primary broadleaved)	Broadleaved monoculture	Broadleaved mixture	Open (cleared)	Heathland
Litter layer	0.05 (0.04)	0.05 (0.02)	0.07 (0.05)	0.07 (0.05)	0.05 (0.04)	0.04 (0.02)	0.01 (NA)	NA
Grass	NA	NA	NA	NA	NA	NA	0.01 (0.01)	0.01 (0.003)
F layer	1.25 (0.97)	1.55 (1.20)	1.26 (1.18)	0.90 (0.67)	0.39 (0.50)	0.41 (0.49)	NA	NA
0-5cm depth	0.81 (0.18)	0.56 (0.22)	0.88 (0.36)	0.97 (0.32)	0.79 (0.32)	0.78 (0.28)	1.21 (0.54)	1.05 (0.39)
5-10cm depth	0.52 (0.11)	0.66 (0.39)	0.53 (0.21)	0.53 (0.20)	0.45 (0.14)	0.52 (0.19)	0.57 (0.20)	0.91 (0.13)
10-20cm depth	0.69 (0.13)	1.02 (0.56)	0.73 (0.37)	0.89 (0.55)	0.63 (0.23)	0.65 (0.32)	0.91 (0.39)	1.24 (0.54)
Organic layers total	1.30 (1.00)	1.69 (1.19)	1.32 (1.19)	0.96 (0.68)	0.44 (0.54)	0.46 (0.51)	0.01 (0.01)	0.01 (0.003)
Mineral layers total	2.02 (0.24)	2.24 (0.86)	2.13 (0.92)	2.40 (0.74)	1.88 (0.44)	1.95 (0.76)	2.69 (0.93)	3.20 (0.95)
All layers total	3.33 (0.94)	3.84 (1.58)	3.46 (0.86)	3.36 (0.95)	2.32 (0.67)	2.41 (0.97)	2.70 (0.93)	3.20 (0.95)

Appendix table B.4: Average C:N ratio of different samples. Values are mean ± standard deviation.

Depth	Conifer monoculture	Conifer mixture	Mixture (primary conifer)	Mixture (primary broadleaved)	Broadleaved monoculture	Broadleaved mixture	Open (cleared)	Heathland
Litter layer	47.16 ± 6.08	45.54 ± 14.75	41.11 ± 7.40	45.29 ± 5.50	42.82 ± 5.12	42.83 ± 7.42	29.89 ± NA	NA
Grass	NA	NA	NA	NA	NA	NA	20.93 ± 2.40	21.32 ± 1.60
F layer	27.35 ± 1.14	30.64 ± 9.64	26.61 ± 3.94	24.92 ± 3.30	28.81 ± 8.30	26.13 ± 4.36	NA	NA
0-5cm depth	20.28 ± 2.23	17.47 ± 3.01	20.48 ± 6.08	20.33 ± 6.75	15.87 ± 2.07	14.97 ± 0.85	17.82 ± 4.80	13.54 ± 0.66
5-10cm depth	17.77 ± 2.18	16.80 ± 3.33	19.71 ± 7.68	15.69 ± 1.63	14.75 ± 2.28	14.37 ± 1.12	16.70 ± 40	12.19 ± 1.25
10-20cm depth	16.59 ± 1.75	16.35 ± 6.75	18.45 ± 7.05	14.91 ± 2.64	14.79 ± 2.62	14.13 ± 1.41	13.97 ± 2.59	11.54 ± 1.81

Appendix C: Chapter 4

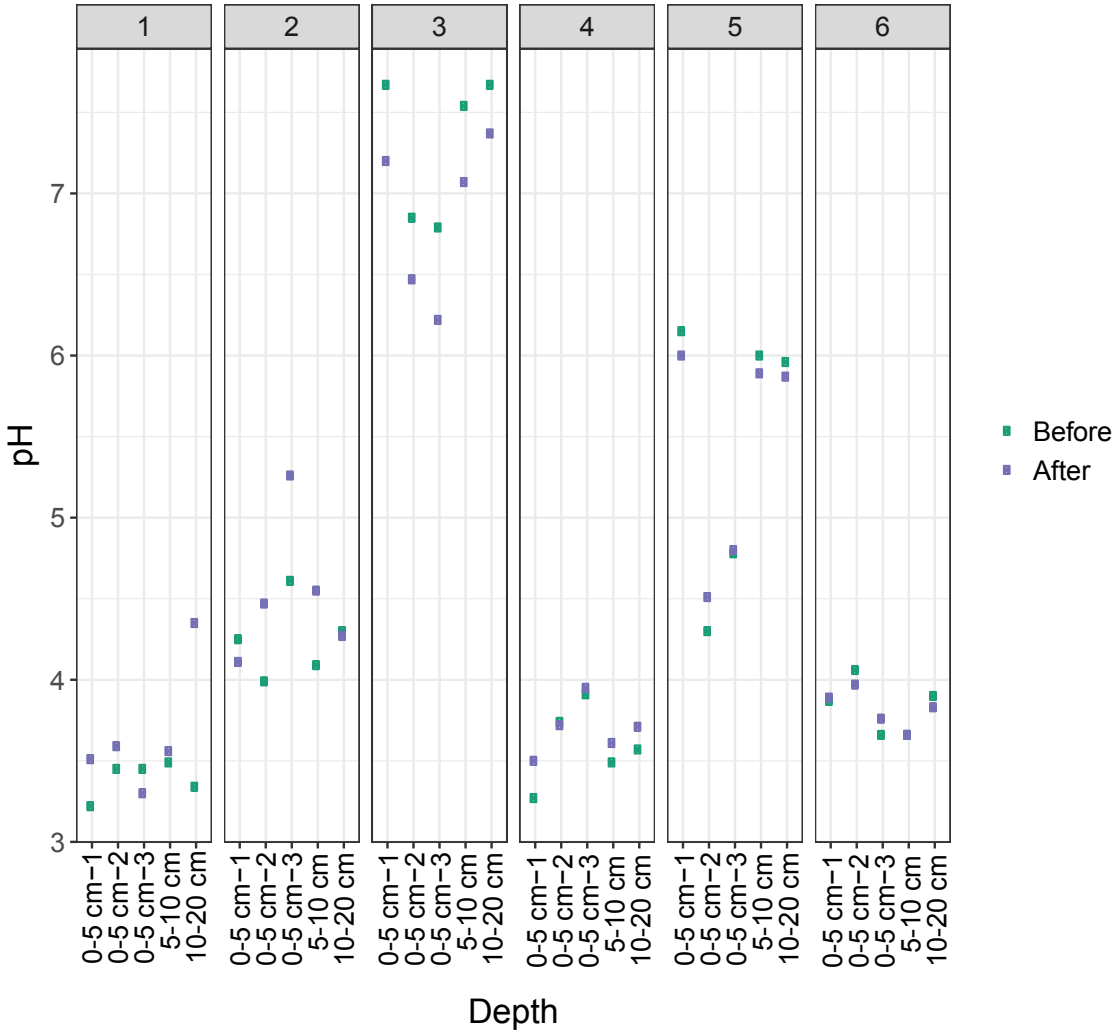
Appendix table C.1: Full information on plots visited.

Category	Species composition (year of planting)	Number of species	Compartment number	Plot no.	Soil information (from Corbett map, 1973)		Area	Average GPS point of sub-plots	
					Soil series	Type of soil		Longitude	Latitude
Conifer monoculture	100% Scots pine (1960)	1	2974 B	7	Methwold	Calcareous	2.65	580928.3	288735
Conifer monoculture	100% Corsican pine (1965)	1	2922 B	8	Santon	Acidic	4.22	580956.7	290745
Conifer monoculture	100% Scots pine (1927)	1	3143 A	9	Worlington	Acidic	5.06	581648.3	291781.7
Conifer monoculture	100% Douglas fir (1928)	1	3523 A	11	Methwold	Calcareous	8.82	580990	287222.5
Conifer monoculture	100% hybrid larch (1999)	1	3409 C	12	Worlington	Acidic	3.96	578502.5	282080
Conifer monoculture	100% Weymouth pine (1964)	1	4501 B	22	Worlington	Acidic	0.53	580797.5	276760
Conifer mixture	42% Grand fir (1966), 40% Corsican pine (1966), 18% Scots pine (1929)	3	2559 A	18	Methwold	Calcareous	5.65	576203.3	291816.7
Conifer mixture	48% Scots pine (1970), 48% Corsican pine (1970), 4% mixed conifers (1926)	3+	3844 A	20	Methwold	Calcareous	9.2	583660	283445
Conifer mixture	40% Corsican pine (1911), 40% Scots pine (1911), 20% Douglas fir (1911)	3	3938 B	21	Methwold	Calcareous	2.66	588717.5	287752.5
Conifer mixture	50% Scots pine (1927), 30% European larch (1927), 20% Douglas fir (1927)	3	2161 B	50	Worlington	Acidic	2.66	579562.5	306040
Conifer mixture	45% Scots pine (1995), 35% Corsican pine (1995), 10% European silver fir (2014), 10% Douglas fir (2014)	4	3793 B	51	Worlington	Acidic	4.55	581785	282435
Conifer mixture	60% Douglas fir (1932, 1980), 40% Grand fir (1932, 1980)	2	2918 A	52	Santon	Acidic	5.49	581130	290962
Broadleaved monoculture	100% sweet chestnut (1979)	1	2716 A	1	Methwold	Calcareous	4.56	579675	293280
Broadleaved monoculture	100% eucalyptus (1980)	1	2934 A	3	Methwold	Calcareous	2.76	580018.8	290111.3
Broadleaved monoculture	100% oak (1933)	1	4207 B	4	Worlington	Acidic	2.76	595350	283942.5
Broadleaved monoculture	100% beech (1932)	1	4282 B	5	Worlington	Acidic	4.55	595650	283410
Broadleaved monoculture	100% birch (1953)	1	4766 C	6	Worlington	Acidic	2.61	583887.5	273995
Broadleaved mixture	50% beech (1949), 20% ash (1949), 25% mixed broadleaves (1900, 1985), 5% oak (1850)	5+	2799 B	13	Methwold	Calcareous	6.33	579495	289457.5
Broadleaved mixture	51% beech (1939), 29% Sycamore (1900), 20% oak (1900)	3	3542 B	14	Methwold	Calcareous	3.86	582744	286330
Broadleaved mixture	50% mixed broadleaves (1975), 25% lime (1966), 25% Sycamore (1966)	3+	4257 A	15	Worlington	Acidic	3.21	597100	283902.5
Broadleaved mixture	49% oak (1970), 33% beech (1960), 11% ash (1970), 7% Sycamore (1970)	4	4264 A	16	Methwold	Calcareous	5.92	598175	284430

Broadleaved mixture	80% beech (1951, 1960), 11% birch (1951), 9% Sycamore (1951)	3+	4624 B	17	Worlington	Acidic	3.43	581375	272940
Mixed (primary conifer)	53% Scots pine (1932), 26% mixed broadleaves (1932), 21% ash (1932)	3+	2922 A	28	Santon	Acidic	9.38	580764	290822
Mixed (primary conifer)	60% Scots pine (1930), 30% Sycamore (1985), 10% sweet chestnut (1975)	3	3141 B	29	Worlington	Acidic	4.72	581530	291937.5
Mixed (primary conifer)	50% European Larch (1926), 30% Scots pine (1926), 20% beech (1926)	3	3843 A	30	Methwold	Calcareous	16.55	583777.5	283507.5
Mixed (primary conifer)	50% Corsican pine (1988), 45% Scots pine (1988), 5% birch (1988)	3	3923 A	31	Freckenham	Acidic	13.87	588940	288252.5
Mixed (primary conifer)	49% Scots pine (1938), 25% oak (1938), 20% beech (1938), 6% sweet chestnut (1938)	4	4228 A	32	Methwold	Calcareous	8.83	597257.5	284752.5
Mixed (primary broad)	40% beech (1907, 1950), 29% European larch (1907), 20% Scots pine (1907), 11% Douglas fir (1907)	4	3703 A	23	Worlington	Acidic	5.29	579165	284820
Mixed (primary broad)	54% beech (1948), 30% Scots pine (1948), 10% oak (1948), 6% birch (1948)	4	2997 A	24	Methwold	Calcareous	7.14	580524	288210
Mixed (primary broad)	40% sweet chestnut (1975), 30% Scots pine (1927), 15% mixed broadleaves (1975), 15% Sycamore (1990)	4+	3140 C	25	Worlington	Acidic	2.76	581757.5	291905
Mixed (primary broad)	50% oak (1934), 40% Scots pine (1934), 10% beech (1934)	3	4223 B	26	Methwold	Calcareous	3.61	597245	285055
Mixed (primary broad)	60% beech (1910), 25% Corsican pine (1955), 15% Scots pine (1955)	3	4775 B	27	Methwold	Calcareous	3.95	583075	274050
Open (cleared)			2514 A	36	Methwold	Calcareous	17.72	577212.5	294127.5
Open (cleared)			2590 A	37	Freckenham	Acidic	13.28	575225	289282.5
Open (cleared)			2711 A	38	Methwold	Calcareous	10.18	578322.5	293305
Open (cleared)			3005 B	40	Freckenham	Acidic	4.42	582170	287920
Open (cleared)			4292 A	41	Methwold	Calcareous	8.21	598240	283240
Heathland			2518 A	33	Methwold	Calcareous	10.3	577465	294125
Heathland			4523 B	34	Worlington	Acidic	2.36	580838	275722
Heathland			Weeting Heath	42	Methwold	Calcareous		575810	288102.5
Heathland			East Wretham	45	Freckenham	Acidic		591544	288162
Heathland			Thetford Heath	44	Methwold	Calcareous		584905	279600

Appendix table C.2: Equivalent grassland and soil series type. Yellow highlighting indicates historical locations where data was compared to Methwold series, blue highlighting indicates locations where data was compared to Worlington series.

Watt, 1940	**Perrin thesis, 1955**			**Breckland Soil Survey, 1973**
Grassland type	**Grassland type**	**Location**	**Genetic group**	**Soil series**
A	A	Profile 35, Lakenheath Warren	Rendzina	Unclear from locations given
B	B	Profile 17, Rakebottom Farm, Elveden	Calcareous brown earth	Methwold
	B	Profile 36, Lakenheath Warren		
	C	Profile 37, Lakenheath Warren		
	C	Profile 44, Wangford Wood	Brown earth	Worlington (no Bt horizon) - Corbett quotes Perrin data
C	C/D	Profile 64, Bridgeham Heath	Sandy bleached terra fusca	Worlington
	D	Profile 62, Garboldisham Heath		
D	D	Profile 41, Warren Wood		Worlington (shallow phase) - Corbett quotes Perrin data
E/F	F	Profile 28, Santon Downham	Humus podsol	Redlodge



Appendix figure C.1: Difference in pH before and after drying.

Appendix D: Chapter 5

Appendix table D.1: Interception ratios from grasslands for different rainfall events.

Interception ratio (%)			Dominant species	Rainfall intensity (mm/h)	Annual precipitation (mm)	Temperature (°C)	Humidity	Notes	Reference
4.2 mm event	6.9 mm event	Average							
50	35	42.5	*Calamagrostis instermedia*	2	1300	6		~30 cm tall	Ochoa-Sánchez, Crespo, & Célleri (2018) [211]
7.4	4.8	6.1	*Kobresia pygmaea* and *Kobresia humilis*		250-367	-5	53-59%	Low vegetation coverage (32%)	Genxu et al. (2012) [209]
10	6.8	8.4	*Kobresia pygmaea* and *Kobresia humilis*		250-367	-5	53-59%	High vegetation coverage (84%)	Genxu et al. (2012) [209]
85	79	82	*Stipa tenacissima*	6	300	8	80%		Domingo et al. (1998) [454]
90	87	88.5	*Stipa tenacissima*	6	300	12	63%		Domingo et al. (1998) [454]
13	8	10.5	*Chionochloa rigida*	0.8			84-100%	Winter	Campbell & Murray (1990) [210]
14	9	11.5	*Chionochloa rigida*	0.8			84-100%	Summer	Campbell & Murray (1990) [210]

Appendix table D.2: Times for which stomatal resistance values were reported in literature.

Reference	Species	Lower time	Upper time	Values
Mokotedi (2010) [455]	Eucalyptus	600	1600	Overall mean reported
Aspelmeier & Leuschner (2004) [456]	Birch	1000	1700	Overall mean reported
Beerling (1997)	Scots pine	Not reported		Overall mean reported
Matyssek & Schulze (1987) [457]	Larch	Not reported		Overall mean reported
Harding et al. (1992) [247]	Ash	900	1600	All times on graph
Harding et al. (1992) [247]	Beech	900	1500	All times on graph
Roberts & Rosier (1994) [458]	Ash	900	1500	All times on graph
Roberts & Rosier (1994) [458]	Beech	900	1500	All times on graph
Sellin & Lubenets (2010) [459]	Birch	700	1700	All times on graph
Elias (1979) [460]	Field maple, hornbeam, oak	515	1815	All times on graph
Hall (1996) [248]	Poplar	730	1930	All times on graph
Losch (1982) [461]	Sweet chestnut	900	1830	All times on graph

Simplification of the Penman-Monteith equation using constant values

I simplified the standard equation as follows (largely following the FAO guidance for a grass reference crop[212], although retaining the r_s term so that I could adapt the equation for different vegetation).

Substitution of $\rho_a c_p$

The psychometric constant (γ) is defined as:

$$\gamma = \frac{C_p P}{\varepsilon \lambda} \quad (1)$$

where,

P = atmospheric pressue (kPa)

λ = latent heat of vaporisation (2.45 MJ kg^{-1})

C_p = specific heat of air at constant pressure (1.013 x 10^{-3} MJ kg^{-1} $^oC^{-1}$)

ε = ratio molecular weight of water vapour/dry air (0.622)

Rearrangement of equation (1) gives:

$$c_p = \frac{\gamma \varepsilon \lambda}{P} \quad (2)$$

The ideal gas law is defined as:

$$\rho_a = \frac{P}{T_{Kv}R} \tag{3}$$

where,

ρ_a = the mean air density at constant pressure (kg m^{-3})

P = atmospheric pressue (kPa)

T_{Kv} = virtual temperature ($1.01(T + 273)$ K)

R = specific gas constant (0.287 kJ kg^{-1} K^{-1})

Therefore,

$$p_a c_p = \frac{P}{T_{Kv}R}\frac{\gamma\varepsilon\lambda}{P} \tag{4}$$

$$= \frac{\gamma\varepsilon\lambda}{T_{Kv}R} \tag{5}$$

Substituting standard values into equation (5):

$$p_a c_p = \frac{\gamma 0.622\lambda}{1.01(T + 273)(0.287)} \tag{6}$$

$$= \frac{\gamma 0.622\lambda}{0.28987(T + 273)} \tag{7}$$

$$= \frac{2.1457\gamma\lambda}{(T + 273)} \tag{8}$$

Substituting equation (8) into equation (6) of the main text:

$$\lambda ET = \frac{\Delta(R_n - G) + \frac{2.1457\gamma\lambda \times (e_s - e_a)}{(T + 273) \times r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)} \tag{9}$$

Standardisation of units of the Penman-Monteith equation

The units of each component of the equation are as follows.

$$\Delta = \frac{\text{kPa}}{^{o}\text{C}} \tag{1}$$

$$(R_n - G) = \left(\frac{\text{MJ}}{\text{m}^2 \times \text{day}}\right) \tag{2}$$

$$p_a c_p = \frac{\text{kg}}{\text{m}^3} \times \frac{\text{MJ}}{\text{kg} \times {}^{o}\text{C}} \tag{3}$$

$$\frac{(e_s - e_a)}{r_a} = \frac{\text{kPa}}{\text{s/m}} = \frac{\text{kPa} \times \text{m}}{\text{s}} \tag{4}$$

$$\gamma\left(1 + \frac{r_s}{r_a}\right) = \frac{\text{kPa}}{^{o}\text{C}}\left(1 + \frac{\text{s/m}}{\text{s/m}}\right) = \frac{\text{kPa}}{^{o}\text{C}} \tag{5}$$

Substituting equations (1) to (5) into equation (6) of the main text:

$$\frac{\frac{\text{kPa}}{^{o}\text{C}}\left(\frac{\text{MJ}}{\text{m}^2 \times \text{day}}\right) + \left(\frac{\text{kg}}{\text{m}^3} \times \frac{\text{MJ}}{\text{kg} \times {}^{o}\text{C}}\right)\left(\frac{\text{kPa} \times \text{m}}{\text{s}}\right)}{\frac{\text{kPa}}{^{o}\text{C}} + \frac{\text{kPa}}{^{o}\text{C}}} \tag{6}$$

$$= \frac{\frac{\text{kPa}}{^{o}\text{C}}\left(\frac{\text{MJ}}{\text{m}^2 \times \text{day}}\right) + \left(\frac{\text{kPa} \times \text{MJ}}{\text{m}^2 \times {}^{o}\text{C} \times \text{s}}\right)}{\frac{\text{kPa}}{^{o}\text{C}}} \tag{7}$$

$$= \frac{\frac{\text{kPa}}{^{o}\text{C}}\left(\frac{\text{MJ}}{\text{m}^2 \times \text{day}}\right) + \frac{\text{kPa}}{^{o}\text{C}}\left(\frac{\text{MJ}}{\text{m}^2 \times \text{s}}\right)}{\frac{\text{kPa}}{^{o}\text{C}}} \tag{8}$$

$$\left(\frac{\text{MJ}}{\text{m}^2 \times \text{day}}\right) + \left(\frac{\text{MJ}}{\text{m}^2 \times \text{s}}\right) \tag{9}$$

To convert MJ m^{-2} s^{-1} to MJ m^{-2} day^{-1}, multiply by 86400 (seconds in a day). To convert MJ m^{-2} day^{-1} to mm day^{-1}, divide by λ (the latent heat of vaporisation: to vaporise 1 kg or 0.001 m^3 water you need 2.45 MJ at 20ºC). Substitute unit conversions into equation (7) of the main text:

$$ET = \frac{0.408\Delta(R_n - G) + \frac{2.1457\gamma \times 86400(e_s - e_a)}{(T + 273) \times r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)} \text{ mm day}^{-1} \tag{10}$$

$$= \frac{0.408\Delta(R_n - G) + \frac{86400 \times 2.1457\gamma \times (e_s - e_a)}{(T + 273) \times r_a}}{\Delta + \gamma\left(1 + \frac{r_s}{r_a}\right)} \text{ mm day}^{-1} \tag{11}$$

Calculation of standard parameters for Penman-Monteith evapotranspiration equation

Δ (slope of saturation vapour pressure curve)

$$\Delta = \frac{4098\left[0.6108 \times exp\left(\frac{17.27T}{T+237.3}\right)\right]}{(T+237.3)^2}$$

where,

Δ = slope of saturation vapour pressure curve at air temperature T (kPa $^{o}C^{-1}$)

T = air temperature (^{o}C)

R_n (net radiation)

$$R_n = R_{ns} - R_{nl}$$

where,

R_n = net radiation

R_{ns} = net shortwave radiation

R_{nl} = outgoing net longwave radiation

$$R_{ns} = (1-\alpha)R_s$$

where,

R_{ns} = net solar or shortwave radiation (MJ m^{-2} day^{-1})

α = albedo (0.23 for grass)

R_s = incoming solar radiation (MJ m^{-2} day^{-1})

$$R_s = \left(a_s + b_s\frac{n}{N}\right)R_a$$

where,

R_s = solar or shortwave radiation (MJ m^{-2} day^{-1})

n = actual sunshine duration (hour)

N = maximum possible duration of sunshine (hour)

R_a = extraterrestrial radiation (MJ m^{-2} day^{-1})

a_s = regression constant (the fraction of extraterrestrial radiation reaching the earth on overcast days; a_s= 0.25)

b_s= 0.5

$$R_{nl} = \sigma \left[\frac{{T_{max,K}}^4 + {T_{min,K}}^4}{2}\right] \left(0.34 - 0.14\sqrt{e_a}\right) \left(1.35 \frac{R_s}{R_{so}} - 0.35\right)$$

where,

R_{nl} = outgoing net longwave radiation

σ = Stefan-Boltzmann constant (4.903 x 10^{-9} MJ K^{-4} m^{-2} day^{-1})

$T_{max,K}$ = maximum absolute temperature during 24-hour period (K = ºC+273.16)

$T_{min,K}$ = minimum absolute temperature during 24-hour period (K = ºC+273.16)

e_a = actual vapour pressure (kPa)

R_s = solar or shortwave radiation (MJ m^{-2} day^{-1})

R_{so} = clear-sky radiation (MJ m^{-2} day^{-1})

$$R_{so} = (0.75 + 2 \times 10^{-5} \times z) \times R_a$$

where,

R_{so} = clear-sky radiation (MJ m^{-2} day^{-1})

z = elevation (m)

R_a = extraterrestrial radiation (MJ m^{-2} day^{-1})

G (soil heat flux)

$$G = 0.07\left(T_{m,i+1} - T_{m,i-1}\right)$$

where,

G = soil heat flux (MJ m^{-2} day^{-1})

$T_{m,i+1}$ = Mean air temperature of next month (ºC)

$T_{m,i-1}$ = Mean air temperature of previous month (ºC)

e_s (mean saturation vapour pressure)

$$e_s = \frac{e^o(T_{max}) + e^o(T_{min})}{2}$$

where,

e_s = mean saturation vapour pressure (kPa)

$e^o(T)$ = saturation vapour pressure at air temperature T (kPa)

$$e^o(T) = 0.6108 \times exp\left(\frac{17.27T}{T + 237.3}\right)$$

where,

$e^o(T)$ = saturation vapour pressure at air temperature T (kPa)

T = air temperature (°C)

γ (psychrometric constant)

$$\gamma = \frac{C_p P}{\varepsilon \lambda}$$

where,

γ = psychrometric constant (kPa $^oC^{-1}$)

P = atmospheric pressue (kPa)

λ = latent heat of vaporisation (2.45 MJ kg^{-1})

C_p = specific heat of air at constant pressure (1.013 x 10^{-3} MJ kg^{-1} $^oC^{-1}$)

ε = ratio molecular weight of water vapour/dry air (0.622)

Therefore,

$$\gamma = (0.665 \times 10^{-3})\, P$$

$$P = 101.3\left(\frac{293 - 0.0065z}{293}\right)^{5.26}$$

where,

P = atmospheric pressue (kPa)

z = elevation (m)

Calculation of aerodynamic resistance

Following Mu et al. (2011) [214] (equation 21):

$$r_a = \frac{rh \times rr}{rh + rr}$$

$$rh = \frac{1}{gl_{bl}}$$

$$rr = \frac{p_a \times C_p}{4 \times \sigma \times {T_i}^3}$$

where,

r_a = aerodynamic resistance (s m^{-1})

gl_bl = leaf-scale boundary layer conductance, = gl_sh (leaf conductance to sensible heat per unit LAI) (m s^{-1})

p_a = air density

C_p = specific heat capacity of air

σ = Stefan-Boltzmann constant (5.67 x 10^{-8} W m^{-2} K^{-4}, note different units and value to *Calculation of standard parameters for Penman-Monteith evapotranspiration equation* above)

T_i = average temperature (°C)

gl_sh = 0.04 for evergreen needleleaf forest; gl_sh = 0.01 for deciduous broadleaved forest; gl_sh = 0.02 for grassland.

As

$$p_a C_p = \frac{2.1457\gamma\lambda}{(T + 273)}$$

$$rr = \frac{\frac{2.1457\gamma \times 2.45}{(T + 273)}}{4 \times (5.67 \times 10^{-8}) \times {T_i}^3}$$

Whereas I divided the Penman-Monteith equation by the latent heat of vaporisation term, this is not necessary in this instance as it is used to estimate r_a, which is measured in s/m, and is already accounted for (see Standardisation of units of the Penman-Monteith equation, above).

Appendix E: Chapter 6

Appendix table E.1: Target audiences identified in the survey outreach plan and example organisations through which they could be contacted, or ways in which they could be informed about the survey.

Target audience	Example organisations to contact or means of informing about survey
Local residents	Thetford Forest Discovery Pass members, schools, libraries
Specialist interests/hobbies	Local wildlife trusts/organisations, cycling groups, walking/rambling groups, forest friends group, local heritage society
People working/volunteering in the forest	Forestry Commission employees, volunteers
Event organisers	Running clubs, cycling events
Local businesses	Activity groups in the forest, e.g. 'Go Ape' treetop adventure course
Occasional visitors (non-local)	Flyers/posters in all main forest parking areas
Local authorities	Local councils and parish councils

*Appendix table E.2: Description of covariates and assigned distance classes. Unless specified, information is from the Forestry Commission databases used with permission. River, road, settlement and elevation data are downloaded from OS OpenData (*Contains OS data © Crown copyright and database right (2017)*). Soil data © Cranfield University (NSRI) used with permission. Heritage designations © Historic England (2017). (Contains Ordnance Survey data © Crown copyright and database right (2017)). Information on heritage features from Norfolk and Suffolk County Councils Historic Environment Records, provided to the Forestry Commission.*

Group: Point features with small influence	
Classes: distances of 0-100 m, 100-500 m, >500 m	
Covariate	***Description***
Information source	Information board/point, interpretation board
Recreation feature	Seat, bench, picnic table/site, barbeque
Play feature/area	Play area, adventure playground, den building site, sculpture
Heritage feature	Flint mine, monument, bell barrow, building
Recreation route	Forestry Commission marked route, public rights of way (e.g. footpath, bridleway, national trail)
Fire route	Forestry Commission trackway system used extensively by public for access
Sports/activity feature	'Go Ape' treetop adventure course, bike pit, archery area, paintball, dog agility, motorcycle area
Toilet	Toilet block
Hide	Wildlife hide
Food outlet	Café, snack shop, ice cream van
Arboretum	Lynford arboretum
Group: Point features with large influence	
Classes: distances of 0-100 m, 100-500 m, 500 m-1 km, >1 km	
Covariate	***Description***
River	Main rivers that run through or alongside the forest: Little Ouse, Thet, Wissey, Lark
Heritage designation	Scheduled ancient monuments, parks and gardens, listed buildings
Group: Access categories	
Classes: distances of 0-100 m, 100-500 m, 500 m-1 km, 1-2 km, 2-5 km, >5 km	
Covariate	***Description***
Road	A, B, local or minor road
Car park	Forestry Commission car park
Settlement	Group of at least 5 buildings no more than 150 m apart.
Access point	Areas commonly used for parking vehicles to access the forest, e.g. laybys at the end of a forest track
Group: Landscape features	
Classes: *See individual descriptions*	
Covariate	***Description***
Elevation	Classified in 10 m intervals from 0 to 60 m. (Data from OS Terrain 50, converted to shapefile of category classes)
Soil	Classified as calcareous, acidic, peat or disturbed ground. From 1973 Corbett soil map.
Access	Classified as open access or non-open access.
Fenced	Classified as fenced or not fenced. Areas visited by people specifically because they offer a secure perimeter (e.g. for dog walking)

Appendix table E.3: Land management options in the Thetford Forest landscape.

Tier 1 land management option	Tier 2 land management option	Number of compartments in landscape	Total area in landscape (ha)	Percentage of landscape area
Conifer monoculture	Corsican pine monoculture	18213	8033.84	41.16
	Scots pine monoculture	7255	1854.25	9.50
	Douglas fir monoculture	740	239.88	1.23
	Larch monoculture (hybrid larch; Japanese larch)	361	100.64	0.52
	Other conifer monoculture	368	95.33	0.49
Conifer mixture		6062	2130.19	10.91
Broadleaved monoculture	Birch monoculture	467	98.88	0.51
	Sweet chestnut monoculture	27	7.69	0.04
	Other broadleaved monoculture	2683	524.64	2.69
Broadleaved mixture		4887	818.59	4.19
Mixture (conifer and broadleaved)	Mixed species; largest percentage area conifer	7020	1961.57	4.40
	Mixed species; largest percentage area broadleaved	3712	858.31	10.05
Open	Open	6140	1210.26	6.20
Arboretum		61	7.58	0.04
Unplanted, failed crop or bare ground		1482	497.38	2.55
Visitor centre		88	13.73	0.07
Open water		205	22.96	0.12
Other	Agriculture	299	50.56	0.26
	Archaeological sites	178	28.05	0.14
	Campsite	98	24.52	0.13
	Car parks/picnic areas	288	33.34	0.17
	Other recreation	145	32.08	0.16
	Other	537	75.18	0.39
Non-FC land		3902	800.51	4.10
TOTAL		**65218**	**19519.97**	**100**

Appendix table E.4: Aggregated responses to survey questions.

Perceived importance of ecosystem services (all respondents)	Recreation	Wildlife	Heritage	Scenic
Very important	101	105	60	101
Quite important	50	39	52	49
Neither important nor unimportant	5	11	39	3
Quite unimportant	2	4	9	6
Very unimportant	4	3	1	2
Not Given	6	6	7	7

Perceived importance of ecosystem services (subset by respondents that contributed mapping to each ecosystem service)	Recreation	Wildlife	Heritage	Scenic
Very important	99	73	28	57
Quite important	49	17	18	25
Neither important nor unimportant	4	5	11	0
Quite unimportant	2	2	2	3
Very unimportant	3	2	1	1
Not Given	5	2	1	2
Total	162	101	61	88

Main use of the forest	Frequency
Cycling	23
Exercise for fitness (e.g. running jogging)	5
Family days out	43
Horse riding	2
Not Given	5
Other	11
Walking (with dog)	32
Walking/hiking (no dog)	21
Wildlife watching/Natural history	26

Gender	Frequency
Female	80
Male	81
Not Given	7

Age	Frequency
18-35	31
36-50	76
51-65	36
Above 65	20
Not Given	5

Visit rate	Frequency
Regularly (more than once a week)	53
Often (more than once a month)	64
Occasionally (more than once a year)	43
Rarely (once or a few times ever)	2
Not Given	6

Appendix F: Chapter 7

Trait database

Trait information was collated from various sources (see table). Nest site individual categories are binary, foraging strata individual categories are estimated percentage use. Body mass, migratory status, nest site (individual categories – ground/cavities/other vegetation), diet category, foraging strata (individual categories – ground/understorey/mid-high vegetation/canopy/aerial) were included in the calculation of functional diversity metrics. Traits with more than one category were weighted accordingly [390,391]. Body mass, migratory status, nest site (overall category), diet category, foraging strata (overall category) were used in RLQ and fourth-corner analysis. UK conservation status and migratory status were used to separate out hierarchical partitioning of variables for species-specific models. I created the overall category for nest site by simply joining together categories if birds used more than one type of nest site. For foraging strata, I created an overall category similar to that used in the Elton traits database to define the diet category: overall category was assigned as the dominant category where one category had more than 50% of estimated usage. Ground and understorey dominant categories were grouped together into Ground_low; mid-high and canopy vegetation were grouped together into Mid-High. If there was no dominant category but the percentages were split between ground and understorey it was assigned Ground_low; if percentages were split between mid-high vegetation and canopy it was assigned Mid-high. If the percentages were split further across these categorisations and there was no dominant category, it was assigned as Multi.

Appendix table F.1: Trait database. SCPTs corresponds to subcompartments.

Species	Number of SCPTs with presence	UK conservation status[$]	Body mass (g)[$]	Migratory status[$]	Nest site[+]				Diet category*	Foraging strata*					
					Ground	Cavities	Other vege-tation	Overall category		Ground	Under-storey	Mid-high vegetation	Canopy	Aerial	Overall category
Blackbird	151	Green	101.8	Resident	0	0	1	Other_veg	Omnivore	60	20	20	0	0	Ground_low
Blackcap	358	Green	17.7	Migrant	0	0	1	Other_veg	Omnivore	0	0	100	0	0	Mid-high
Blue Tit	264	Green	10.9	Resident	0	1	0	Cavities	Omnivore	10	30	30	30	0	Multi
Bullfinch	16	Amber	22.5	Resident	0	0	1	Other_veg	PlantSeed	0	50	50	0	0	Multi
Buzzard	23	Green	828.2	Resident	0	0	1	Other_veg	VertFishScav	100	0	0	0	0	Ground_low
Carrion Crow	193	Green	508.7	Resident	0	1	1	Cavities_ Other_veg	VertFishScav	90	0	0	0	10	Ground_low
Chaffinch	448	Green	21.8	Resident	0	0	1	Other_veg	Invertebrate	40	30	30	0	0	Multi
Chiffchaff	332	Green	7.7	Migrant	1	0	1	Ground_ Other_veg	Invertebrate	25	25	25	25	0	Multi
Coal Tit	376	Green	9.1	Resident	0	1	0	Cavities	Omnivore	100	0	0	0	0	Ground_low
Cuckoo	30	Red	114.3	Migrant	0	0	1	Other_veg	Invertebrate	20	20	40	20	0	Multi
Curlew	1	Red	783.9	Partial/short distance migrant	1	0	0	Ground	Omnivore	100	0	0	0	0	Ground_low
Dunnock	60	Amber	21.2	Resident	0	0	1	Other_veg	Omnivore	100	0	0	0	0	Ground_low
Firecrest	15	Green	5.4	Partial/short distance migrant	0	0	1	Other_veg	Invertebrate	0	50	50	0	0	Multi
Garden Warbler	63	Green	17.2	Migrant	0	0	1	Other_veg	Omnivore	0	60	20	20	0	Ground_low
Goldcrest	311	Green	5.3	Partial/short distance migrant	0	0	1	Other_veg	Invertebrate	0	50	50	0	0	Multi
Goldfinch	18	Green	15.8	Partial/short distance migrant	0	0	1	Other_veg	PlantSeed	20	60	20	0	0	Ground_low
Great Spotted Woodpecker	33	Green	78.7	Resident	0	1	0	Cavities	Omnivore	0	20	40	30	10	Multi
Great Tit	225	Green	18.6	Resident	0	1	0	Cavities	Omnivore	0	20	60	20	0	Mid-high
Green Woodpecker	26	Green	188.9	Resident	0	1	0	Cavities	Invertebrate	100	0	0	0	0	Ground_low

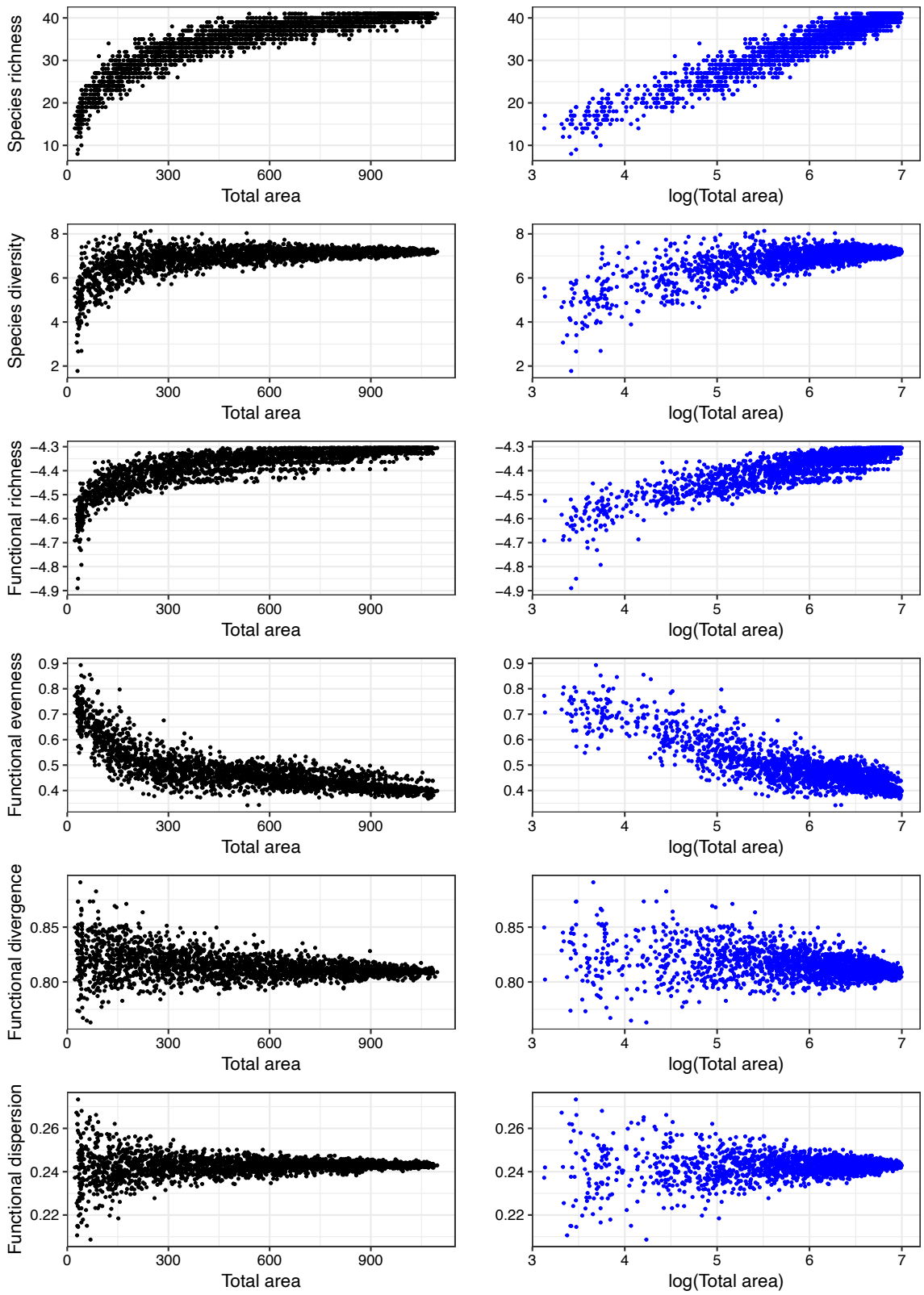
Greenfinch	8	Green	27.7	Resident	0	0	1	Other_veg	PlantSeed	40	30	30	0	0	Multi
Jackdaw	13	Green	231.8	Resident	0	1	0	Cavities	Omnivore	50	20	20	10	0	Multi
Jay	70	Green	166.8	Resident	0	0	1	Other_veg	Omnivore	60	20	20	0	0	Ground_low
Kestrel	3	Amber	205.5	Resident	0	1	1	Cavities_ Other_veg	VertFishScav	80	10	10	0	0	Ground_low
Linnet	45	Red	18.8	Migrant	0	0	1	Other_veg	PlantSeed	60	20	20	0	0	Ground_low
Long-tailed Tit	86	Green	7.8	Resident	0	0	1	Other_veg	Invertebrate	10	40	10	40	0	Multi
Magpie	26	Green	212.9	Resident	0	0	1	Other_veg	VertFishScav	70	10	10	0	10	Ground_low
Marsh Tit	36	Red	10.7	Resident	0	1	0	Cavities	Omnivore	0	20	80	0	0	Mid-high
Meadow Pipit	6	Amber	18.9	Partial/short distance migrant	1	0	0	Ground	Invertebrate	70	20	10	0	0	Ground_low
Mistle Thrush	24	Red	125.9	Resident	0	0	1	Other_veg	Omnivore	60	20	10	10	0	Ground_low
Nuthatch	67	Green	22.1	Resident	0	1	0	Cavities	Invertebrate	33.3	33.3	33.3	0	0	Multi
Pheasant	110	Not assessed	1190.0	Resident	1	0	0	Ground	PlantSeed	100	0	0	0	0	Ground_low
Red-legged Partridge	12	Not assessed	490.0	Resident	1	0	0	Ground	PlantSeed	100	0	0	0	0	Ground_low
Robin	514	Green	19.0	Resident	1	0	1	Ground_ Other_veg	Omnivore	50	50	0	0	0	Ground_low
Siskin	53	Green	12.9	Migrant	0	0	1	Other_veg	PlantSeed	0	50	50	0	0	Multi
Skylark	27	Red	38.6	Partial/short distance migrant	1	0	0	Ground	PlantSeed	100	0	0	0	0	Ground_low
Song Thrush	179	Red	75.0	Resident	0	0	1	Other_veg	Omnivore	100	0	0	0	0	Ground_low
Spotted Flycatcher	4	Red	14.5	Migrant	0	1	1	Cavities_ Other_veg	Invertebrate	60	40	0	0	0	Ground_low
Stock Dove	16	Amber	326.3	Resident	0	1	0	Cavities	PlantSeed	80	20	0	0	0	Ground_low
Stonechat	3	Green	15.8	Partial/short distance migrant	1	0	1	Ground_ Other_veg	Invertebrate	100	0	0	0	0	Ground_low
Tree Pipit	45	Red	21.6	Migrant	1	0	0	Ground	Invertebrate	100	0	0	0	0	Ground_low
Treecreeper	71	Green	8.8	Resident	0	1	1	Cavities_ Other_veg	Invertebrate	40	30	30	0	0	Multi
Turtle Dove	6	Red	156.8	Migrant	0	0	1	Other_veg	Omnivore	100	0	0	0	0	Ground_low

Whitethroat	69	Green	13.8	Migrant	0	0	1	Other_veg	Invertebrate	0	100	0	0	0	Ground_low
Willow Warbler	142	Amber	8.9	Migrant	1	0	1	Ground_ Other_veg	Invertebrate	0	0	30	70	0	Mid-high
Woodlark	29	Green	30.0	Partial/short distance migrant	1	0	0	Ground	Omnivore	100	0	0	0	0	Ground_low
Woodpigeon	403	Green	507.4	Resident	0	0	1	Other_veg	PlantSeed	80	20	0	0	0	Ground_low
Wren	737	Green	9.9	Resident	0	1	1	Cavities_ Other_veg	Invertebrate	50	50	0	0	0	Ground_low
Yellowhammer	117	Red	25.9	Resident	1	0	1	Ground_ Other_veg	PlantSeed	100	0	0	0	0	Ground_low

*Data gathered from Elton Traits database [462]. For nuthatch, I corrected values to be 33.3 instead of 33.

[+]Data gathered from Oliveira Hagen et al. [463]. I amalgamated the cavities in cliff, rocks, ground and tree cavities into one category ‘cavities’. I removed the artefacts nest column as this database was created for the study of urban birds, and artificial structures are not generally present in the forest.

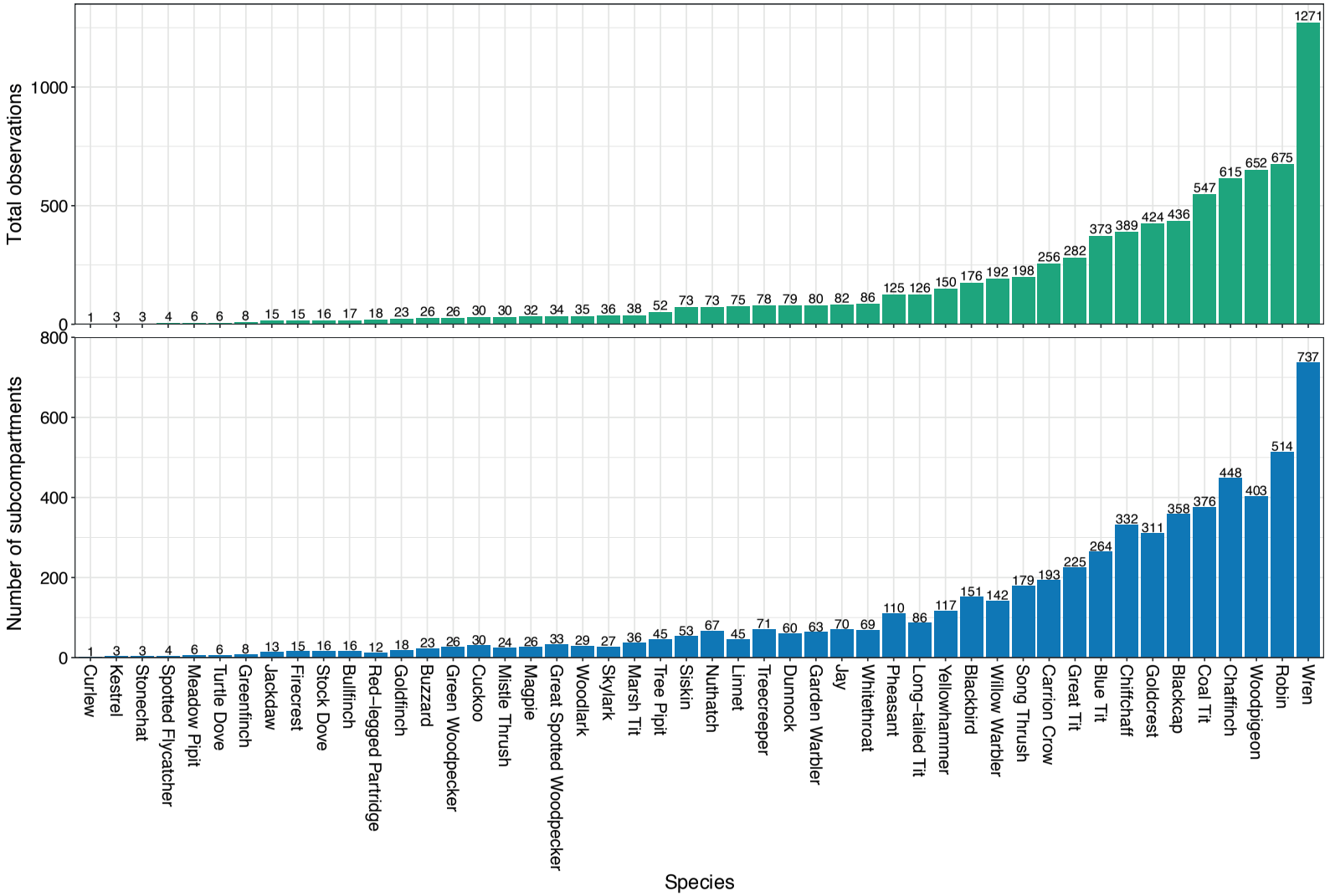
[$]Dat a gathered from BTO birdfacts [464]. For body mass, where there was great sexual dimorphism, the average was taken (curlews, pheasants). Migratory status was refined to the populations in Thetford Forest using local expert knowledge (Greg Conway, pers. comm.)



Appendix figure F.1: Relationship between total area and diversity metrics.

Appendix table F.2: Correlation coefficient between variables. Blue shading indicates values greater than |0.7|. Top canopy height, gap fraction, vertical evenness, canopy density and age class were all correlated to each other to a high degree.

	Top canopy height (5 m)	**Gap fraction (0.5 m)**	**Vertical evenness**	**Horizontal heterogeneity (10 m)**	**Canopy density**	**Shrub density**	**Broad management type**	**Total area (log)**	**Age class**
Top canopy height (5 m)		-0.859	0.761	0.125	0.860	-0.163	0.504	0.225	0.948
Gap fraction (0.5 m)	-0.859		-0.921	-0.327	-0.942	-0.266	0.575	-0.262	0.919
Vertical evenness	0.761	-0.921		0.260	0.801	0.315	0.435	0.185	0.790
Horizontal heterogeneity (10 m)	0.125	-0.327	0.260		0.308	0.349	0.331	0.420	0.309
Canopy density	0.860	-0.942	0.801	0.308		0.147	0.485	0.363	0.928
Shrub density	-0.163	-0.266	0.315	0.349	0.147		0.325	0.004	0.422
Broad management type	0.504	0.575	0.435	0.331	0.485	0.325		0.319	0.642
Total area (log)	0.225	-0.262	0.185	0.420	0.363	0.004	0.319		0.330
Age class	0.948	0.919	0.790	0.309	0.928	0.422	0.642	0.330	



Appendix figure F.2: Total observations (sum of the max counts) and number of subcompartments in which all bird species were observed. Species are ordered by increasing total number of observations. See main text for where certain species were included (e.g. at least 15 subcompartments for species-specific models).

Appendix G: Chapter 8

Appendix table G.1: All ecosystem service values for comprehensive management categories. CCF corresponds to continuous-cover forestry.

Management category	Species	Management type	Timber	Carbon	Deer	Soil quality			Water	Wildlife	Recreation	Scenic	Heritage
						Carbon	Nitrogen	C:N					
Conifer monoculture	Corsican pine	Clearfell	13.96	324.77	-714866	18.92	0.56	25.83	-60.54	0.00E+00	3.65E-02	7.95E-02	0.00E+00
		CCF	13.96	359.79	-714866	18.92	0.56	25.83	-60.54	0.00E+00	3.65E-02	7.95E-02	0.00E+00
	Douglas fir	Clearfell	12.14	390.88	-426880	18.92	0.56	25.83	-60.54	1.00E+00	1.00E+00	1.00E-04	6.31E-01
		CCF	12.14	422.80	-426880	18.92	0.56	25.83	-60.54	1.00E+00	1.00E+00	1.00E-04	6.31E-01
	Hybrid larch	Clearfell	10.10	250.85	-547132	18.92	0.56	25.83	-60.54	1.00E+00	9.99E-01	3.71E-01	5.63E-01
		CCF	10.10	256.72	-547132	18.92	0.56	25.83	-60.54	1.00E+00	9.99E-01	3.71E-01	5.63E-01
	Japanese larch	Clearfell	10.10	264.80	-547132	18.92	0.56	25.83	-60.54	1.00E+00	9.99E-01	3.71E-01	5.63E-01
		CCF	10.10	270.87	-547132	18.92	0.56	25.83	-60.54	1.00E+00	9.99E-01	3.71E-01	5.63E-01
	Other conifer	Clearfell	11.72	315.04	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
		CCF	11.72	371.06	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
	Scots pine	Clearfell	9.98	283.75	-341980	18.92	0.56	25.83	56.80	8.60E-03	2.74E-02	9.12E-01	9.96E-01
		CCF	9.98	348.42	-341980	18.92	0.56	25.83	56.80	8.60E-03	2.74E-02	9.12E-01	9.96E-01
	Serbian spruce	Clearfell	6.89	204.56	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
		CCF	6.89	260.65	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
	Western hemlock	Clearfell	16.00	409.18	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
		CCF	16.00	498.19	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
	Western red cedar	Clearfell	14.00	374.76	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
		CCF	14.00	443.14	-714866	18.92	0.56	25.83	-60.54	2.92E-02	9.32E-01	6.72E-01	6.00E-03
Conifer mixture	Hybrid larch pioneer	Clearfell	10.75	286.70	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
		CCF	11.16	346.89	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
	Scots pine pioneer	Clearfell	10.69	307.44	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
		CCF	11.11	379.55	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01

Conifer mixture - underplanting	Hybrid larch pioneer	Clearfell	10.75	235.64	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
		CCF	10.75	294.19	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
	Scots pine pioneer	Clearfell	10.69	240.14	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
		CCF	10.69	340.04	-326912	19.00	0.58	25.36	-60.54	8.95E-01	0.00E+00	1.00E+00	6.18E-01
Conifer and broadleaved mixture	Scots pine & beech	CCF	7.93	326.80	-249159	18.05	0.58	25.27	-13.42	0.00E+00	9.72E-01	1.70E-01	9.93E-01
	Scots pine & oak	CCF	6.93	298.43	-249159	18.05	0.58	25.27	-13.42	0.00E+00	9.72E-01	1.70E-01	9.93E-01
Broadleaved monoculture	Birch	CCF	4.00	248.44	-705671	17.52	0.54	23.41	191.24	9.64E-01	5.00E-04	4.83E-01	1.32E-02
	Eucalyptus	CCF	26.05	361.01	-705671	17.52	0.54	23.41	33.70	8.94E-01	9.99E-01	2.08E-02	0.00E+00
	Other broadleaved	CCF	6.23	251.61	-705671	17.52	0.54	23.41	33.70	8.94E-01	9.99E-01	2.08E-02	0.00E+00
	Sweet chestnut	CCF	3.91	229.63	-705671	17.52	0.54	23.41	33.70	2.78E-01	2.56E-01	1.00E+00	7.40E-03
Broadleaved mixture	Birch & sweet chestnut pioneer	CCF	4.33	256.02	-705671	17.49	0.56	22.49	33.70	1.19E-01	2.17E-01	8.10E-01	1.00E+00
	Birch pioneer	CCF	4.44	262.62	-705671	17.49	0.56	22.49	33.70	1.19E-01	2.17E-01	8.10E-01	1.00E+00
	No pioneer	CCF	4.58	267.35	-705671	17.49	0.56	22.49	33.70	1.19E-01	2.17E-01	8.10E-01	1.00E+00
	Sweet chestnut pioneer	CCF	4.42	257.92	-705671	17.49	0.56	22.49	33.70	1.19E-01	2.17E-01	8.10E-01	1.00E+00
Open	Open	Open	0.00	0.00	0	5.05	0.29	14.65	327.53	9.39E-01	9.93E-01	8.51E-01	9.60E-01

Appendix table G.2: All management options included in the multi-criteria analysis, and the corresponding categories used for each ecosystem service. The cultural group includes wildlife, recreation, scenic beauty, heritage. The mean was calculated where multiple groups are listed. CCF corresponds to continuous-cover forestry.

Management group	Primary species	Management type	Timber	Carbon	Deer	Soil	Water	Cultural
Conifer monoculture	Corsican pine	Clearfell	Corsican pine monoculture	Corsican pine monoculture clearfell	Other conifer monoculture	Conifer monoculture	Conifer	Corsican pine monoculture
		CCF	Corsican pine monoculture	Corsican pine monoculture CCF	Other conifer monoculture	Conifer monoculture	Conifer	Corsican pine monoculture
	Douglas fir	Clearfell	Douglas fir monoculture	Douglas fir monoculture clearfell	Douglas fir monoculture	Conifer monoculture	Conifer	Douglas fir monoculture
		CCF	Douglas fir monoculture	Douglas fir monoculture CCF	Douglas fir monoculture	Conifer monoculture	Conifer	Douglas fir monoculture
	Hybrid larch	Clearfell	Hybrid larch monoculture	Hybrid larch monoculture clearfell	Larch monoculture	Conifer monoculture	Conifer	Larch monoculture
		CCF	Hybrid larch monoculture	Hybrid larch monoculture CCF	Larch monoculture	Conifer monoculture	Conifer	Larch monoculture
	Japanese larch	Clearfell	Japanese larch monoculture	Japanese larch monoculture clearfell	Larch monoculture	Conifer monoculture	Conifer	Larch monoculture
		CCF	Japanese larch monoculture	Japanese larch monoculture CCF	Larch monoculture	Conifer monoculture	Conifer	Larch monoculture
	Other conifer	Clearfell	Other conifer monoculture	Other conifer monoculture clearfell	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
		CCF	Other conifer monoculture	Other conifer monoculture CCF	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
	Scots pine	Clearfell	Scots pine monoculture	Scots pine monoculture clearfell	Scots pine monoculture	Conifer monoculture	Scots pine	Scots pine monoculture
		CCF	Scots pine monoculture	Scots pine monoculture CCF	Scots pine monoculture	Conifer monoculture	Scots pine	Scots pine monoculture
	Serbian spruce	Clearfell	Serbian spruce monoculture	Serbian spruce monoculture clearfell	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
		CCF	Serbian spruce monoculture	Serbian spruce monoculture CCF	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
	Western hemlock	Clearfell	Western hemlock monoculture	Western hemlock monoculture clearfell	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
		CCF	Western hemlock monoculture	Western hemlock monoculture CCF	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
	Western red cedar	Clearfell	Western red cedar monoculture	Western red cedar monoculture clearfell	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture
		CCF	Western red cedar monoculture	Western red cedar monoculture CCF	Other conifer monoculture	Conifer monoculture	Conifer	Other conifer monoculture

Conifer mixture	Hybrid larch pioneer	Clearfell	Hybrid larch, Douglas fir mixture; Hybrid larch, western hemlock mixture; Hybrid larch, western red cedar mixture; Hybrid larch, Japanese cedar mixture; Hybrid larch, Serbian spruce mixture	Hybrid larch, Douglas fir mixture clearfell; Hybrid larch, western hemlock mixture clearfell; Hybrid larch, western red cedar mixture clearfell; Hybrid larch, Japanese cedar mixture clearfell; Hybrid larch, Serbian spruce mixture clearfell	Conifer mixture	Conifer mixture	Conifer	Conifer mixture
		CCF	Hybrid larch, Douglas fir mixture; Hybrid larch, western hemlock mixture; Hybrid larch, western red cedar mixture; Hybrid larch, Japanese cedar mixture; Hybrid larch, Serbian spruce mixture; Hybrid larch, Douglas fir, western hemlock; Hybrid larch, Douglas fir, western red cedar; Hybrid larch, Douglas fir, Japanese cedar; Hybrid larch, western hemlock, western red cedar; Hybrid larch, western hemlock, Japanese cedar; Hybrid larch, western red cedar, Japanese cedar; Hybrid larch, Douglas fir, western hemlock, western red cedar; Hybrid larch, Douglas fir, western hemlock, Japanese cedar; Hybrid larch, Douglas fir, western red cedar, Japanese cedar; Hybrid larch, western hemlock, western red cedar, Japanese cedar; Hybrid larch, Douglas fir, western hemlock, western red cedar, Japanese cedar	Hybrid larch, Douglas fir mixture CCF; Hybrid larch, western hemlock mixture CCF; Hybrid larch, western red cedar mixture CCF; Hybrid larch, Japanese cedar mixture CCF; Hybrid larch, Serbian spruce mixture CCF; Hybrid larch, Douglas fir, western hemlock CCF; Hybrid larch, Douglas fir, western red cedar CCF; Hybrid larch, Douglas fir, Japanese cedar CCF; Hybrid larch, western hemlock, western red cedar CCF; Hybrid larch, western hemlock, Japanese cedar CCF; Hybrid larch, western red cedar, Japanese cedar CCF; Hybrid larch, Douglas fir, western hemlock, western red cedar CCF; Hybrid larch, Douglas fir, western hemlock, Japanese cedar CCF; Hybrid larch, Douglas fir, western red cedar, Japanese cedar CCF; Hybrid larch, western hemlock, western red cedar, Japanese cedar CCF; Hybrid larch, Douglas fir, western hemlock, western red cedar, Japanese cedar CCF	Conifer mixture	Conifer mixture	Conifer	Conifer mixture

	Scots pine pioneer	Clearfell	Scots pine, Douglas fir mixture; Scots pine, western hemlock mixture; Scots pine, western red cedar mixture; Scots pine, Japanese cedar mixture; Scots pine, Serbian spruce mixture	Scots pine, Douglas fir mixture clearfell; Scots pine, western hemlock mixture clearfell; Scots pine, western red cedar mixture clearfell; Scots pine, Japanese cedar mixture clearfell; Scots pine, Serbian spruce mixture clearfell	Conifer mixture	Conifer mixture	Conifer	Conifer mixture
		CCF	Scots pine, Douglas fir mixture; Scots pine, western hemlock mixture; Scots pine, western red cedar mixture; Scots pine, Japanese cedar mixture; Scots pine, Serbian spruce mixture; Scots pine, Douglas fir, western hemlock; Scots pine, Douglas fir, western red cedar; Scots pine, Douglas fir, Japanese cedar; Scots pine, western hemlock, western red cedar; Scots pine, western hemlock, Japanese cedar; Scots pine, western red cedar, Japanese cedar; Scots pine, Douglas fir, western hemlock, western red cedar; Scots pine, Douglas fir, western hemlock, Japanese cedar; Scots pine, Douglas fir, western red cedar, Japanese cedar; Scots pine, western hemlock, western red cedar, Japanese cedar; Scots pine, Douglas fir, western hemlock, western red cedar, Japanese cedar	Scots pine, Douglas fir mixture CCF; Scots pine, western hemlock mixture CCF; Scots pine, western red cedar mixture CCF; Scots pine, Japanese cedar mixture CCF; Scots pine, Serbian spruce mixture CCF; Scots pine, Douglas fir, western hemlock CCF; Scots pine, Douglas fir, western red cedar CCF; Scots pine, Douglas fir, Japanese cedar CCF; Scots pine, western hemlock, western red cedar CCF; Scots pine, western hemlock, Japanese cedar CCF; Scots pine, western red cedar, Japanese cedar CCF; Scots pine, Douglas fir, western hemlock, western red cedar CCF; Scots pine, Douglas fir, western hemlock, Japanese cedar CCF; Scots pine, Douglas fir, western red cedar, Japanese cedar CCF; Scots pine, western hemlock, western red cedar, Japanese cedar CCF; Scots pine, Douglas fir, western hemlock, western red cedar, Japanese cedar CCF	Conifer mixture	Conifer mixture	Conifer	Conifer mixture

Conifer mixture - underplanting	Hybrid larch pioneer	Clearfell	Hybrid larch, Douglas fir mixture; Hybrid larch, western hemlock mixture; Hybrid larch, western red cedar mixture; Hybrid larch, Japanese cedar mixture; Hybrid larch, Serbian spruce mixture	Hybrid larch, Douglas fir underplanting clearfell; Hybrid larch, western hemlock underplanting clearfell; Hybrid larch, western red cedar underplanting clearfell; Hybrid larch, Japanese cedar underplanting clearfell; Hybrid larch, Serbian spruce underplanting clearfell	Conifer mixture	Conifer mixture	Conifer	Conifer mixture
		CCF	Hybrid larch, Douglas fir mixture; Hybrid larch, western hemlock mixture; Hybrid larch, western red cedar mixture; Hybrid larch, Japanese cedar mixture; Hybrid larch, Serbian spruce mixture	Hybrid larch, Douglas fir underplanting CCF; Hybrid larch, western hemlock underplanting CCF; Hybrid larch, western red cedar underplanting CCF; Hybrid larch, Japanese cedar underplanting CCF; Hybrid larch, Serbian spruce underplanting CCF	Conifer mixture	Conifer mixture	Conifer	Conifer mixture
	Scots pine pioneer	Clearfell	Scots pine, Douglas fir mixture; Scots pine, western hemlock mixture; Scots pine, western red cedar mixture; Scots pine, Japanese cedar mixture; Scots pine, Serbian spruce mixture	Scots pine, Douglas fir underplanting clearfell; Scots pine, western hemlock underplanting clearfell; Scots pine, western red cedar underplanting clearfell; Scots pine, Japanese cedar underplanting clearfell; Scots pine, Serbian spruce underplanting clearfell	Conifer mixture	Conifer mixture	Conifer	Conifer mixture
		CCF	Scots pine, Douglas fir mixture; Scots pine, western hemlock mixture; Scots pine, western red cedar mixture; Scots pine, Japanese cedar mixture; Scots pine, Serbian spruce mixture	Scots pine, Douglas fir underplanting CCF; Scots pine, western hemlock underplanting CCF; Scots pine, western red cedar underplanting CCF; Scots pine, Japanese cedar underplanting CCF; Scots pine, Serbian spruce underplanting CCF	Conifer mixture	Conifer mixture	Conifer	Conifer mixture

Conifer and broadleaved mixture	Scots pine & beech	CCF	Mixture, beech & Scots pine	Mixture, beech & Scots pine CCF	Mixture (conifer and broadleaved)	Mixed (primary conifer)	Mixture (conifer and broadleaved)	Mixture (conifer and broadleaved)
	Scots pine & oak	CCF	Mixture, oak & Scots pine	Mixture, oak & Scots pine CCF	Mixture (conifer and broadleaved)	Mixed (primary conifer)	Mixture (conifer and broadleaved)	Mixture (conifer and broadleaved)
Broadleaved monoculture	Birch	CCF	Birch monoculture	Birch monoculture CCF	Broadleaved	Broadleaved monoculture	Birch	Birch monoculture
	Eucalyptus	CCF	Eucalyptus monoculture	Eucalyptus monoculture CCF	Broadleaved	Broadleaved monoculture	Broadleaved	Other broadleaved monoculture
	Other broadleaved	CCF	Other broad monoculture	Other broad monoculture CCF	Broadleaved	Broadleaved monoculture	Broadleaved	Other broadleaved monoculture
	Sweet chestnut	CCF	Sweet chestnut monoculture	Sweet chestnut monoculture CCF	Broadleaved	Broadleaved monoculture	Broadleaved	Sweet chestnut monoculture
Broadleaved mixture	Birch & sweet chestnut pioneer	CCF	Broad mixture, birch & sweet chestnut pioneer	Broad mixture, birch & sweet chestnut pioneer CCF	Broadleaved	Broadleaved mixture	Broadleaved	Pure broadleaved mixture
	Birch pioneer	CCF	Broad mixture, birch pioneer	Broad mixture, birch pioneer CCF	Broadleaved	Broadleaved mixture	Broadleaved	Pure broadleaved mixture
	No pioneer	CCF	Broad mixture, no pioneer	Broad mixture, no pioneer CCF	Broadleaved	Broadleaved mixture	Broadleaved	Pure broadleaved mixture
	Sweet chestnut pioneer	CCF	Broad mixture, sweet chestnut pioneer	Broad mixture, sweet chestnut pioneer CCF	Broadleaved	Broadleaved mixture	Broadleaved	Pure broadleaved mixture
Open	Open	Open	NA	NA	NA	Always open	Heath	Open